5-2010

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Antonin Kusbach
Utah State University

TERRESTRIAL ECOSYSTEM CLASSIFICATION IN THE ROCKY MOUNTAINS,

NORTHERN UTAH

by

Antonin Kusbach

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

Approved:

James N. Long Co-Major Professor	Helga Van Miegroet Co-Major Professor
Karel Klinka Committee Member	Leila M. Shultz Committee Member
Janis L. Boettinger Committee Member	Byron R. Burnham Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2010

ABSTRACT

Terrestrial Ecosystem Classification in the Rocky Mountains, Northern Utah

by

Antonin Kusbach, Doctor of Philosophy

Utah State University, 2010

Major Professors: Dr. James N. Long, Dr. Helga Van Miegroet
Department: Wildland Resources

Currently, there is no comprehensive terrestrial ecosystem classification for the central Rocky Mountains of the United States. A comprehensive classification of terrestrial ecosystems in a mountainous study area in northern Utah was developed incorporating direct gradient analysis, spatial hierarchy theory, the zonal concept, and concepts of diagnostic species and fidelity, together with the biogeoclimatic ecosystem classification approach used in British Columbia, Canada.

This classification was derived from vegetation and environmental sampling of both forest and non-forest ecosystems. The SNOwpack TELemetry (SNOTEL) and The National Weather Service (NWS) Cooperative Observer Program (COOP) weather station network were used to approximate climate of 163 sample plots.

Within the large environmental diversity of the study area, three levels of ecosystem organization were distinguished: (1) macroclimatic – regional climate; (2) mesoclimatic, accounting for local climate and moisture distribution; and (3) edaphic - soil fertility. These three levels represent, in order, the L+1, L, and L-1 levels in a spatial hierarchy.

Based on vegetation physiognomy, climatic data, and taxonomic classification of zonal soils, two vegetation geo-climatic zones were identified at the macroclimatic (L+1) level: (1) montane zone with Rocky Mountain juniper and Douglas-fir; and (2) subalpine zone with Engelmann spruce and subalpine fir as climatic climax species.

A vegetation classification was developed by combining vegetation samples (relevés) into meaningful vegetation units.

A site classification was developed, based on dominant environmental gradients within the subalpine vegetation geo-climatic zone. Site classes were specified and a site grid was constructed. This site classification was coupled with the vegetation classification. Each plant community was associated with its environmental space within the site grid. This vegetation-site overlay allowed ecosystems to be differentiated environmentally and a structure, combining zonal, vegetation, and site classifications, forms a comprehensive ecosystem classification.

Based on assessment of plant communities' environmental demands and site vegetation potential, the comprehensive classification system enables inferences about site history and successional status of ecosystems. This classification is consistent with the recent USDA, Forest Service ECOMAP and Terrestrial Ecological Unit Inventory structure and may serve as a valuable tool not only in vegetation, climatic, or soil studies but also in practical ecosystem management.

(221 pages)

ACKNOWLEDGMENTS

I would like to thank my major professors, Helga Van Miegroet and Jim Long, for their assistance, support, and patience through the entire study process. I would like to thank my mentor, Karel Klinka, for his advice, and mental and professional support. I would also like to thank my committee members, Leila Shultz and Janis Boettinger, for their willingness and invaluable help in the field of botany and soil science; Susan Durham for her statistical consultation; Mary Barkworth for her help in botanical recognition of graminoid species; and Michael Butkus for his help with a field accommodation. This project would not have been possible without the help of many field and laboratory technicians. Thank you.

For financial assistance during the course of my doctoral dissertation I would like to acknowledge: the Utah State University Ecology Center and the USDA Forest Service, Wasatch-Cache National Forests, Forest Supervisor's Office. I also acknowledge USDA Forest Service, Wasatch-Cache National Forests, Logan Ranger District for consultation and providing materials related to my study.

For incredible support outside the academic environment I would like to thank my family and all my friends. Most especially, I am grateful for the help and patience of my wife, Jolly, and support of my parents far away in the Czech Republic, Europe.

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CHAPTER 1

INTRODUCTION

Increasingly, society has to deal with complex challenges in management of natural resources, including changes in land use and climate. A particular challenge is that management of natural resources needs to be sustainable. In light of these challenges, it is desirable to adopt an ecosystem approach to natural resource management rather than attempting to manage individual resources (Bailey 2002). This approach requires classification of units of land into ecologically meaningful and relatively uniform segments.

The need for land classification has long been recognized. Many systems have categorized units of land based on a few, and often one, important ecosystem components, e.g., vegetation, animals, microorganisms or some aspect of the physical environment, such as climate or soils (Pojar et al. 1987). For example, the Köppen classification of climates modified by Trewartha (1968) is entirely a climatic classification. The habitat types (Daubenmire 1952), community types (Mueggler 1988) as well as the potential natural vegetation classifications of Küchler (1969) are classifications based strictly on vegetation. Some systems have combined two or more ecosystems components, e.g., ecoregions (Bailey 1998a, b) and the biogeoclimatic ecosystem classification developed in British Columbia, Canada (Pojar et al. 1987). Thus, for classification and mapping purposes, the ecosystem emphasizes vegetation, geomorphology and soils; its meaning is generally geographic (D. Roberts 2008, personal communication). Currently, however, there is no comprehensive ecosystem classification for the central Rocky Mountains of the United States.

One of the tests of ecosystem classification usefulness is the extent to which it provides insight into factors influencing the distribution of vegetation. In addition to disturbances and biotic interactions (e.g., competition); the physical environment, conceptually represented by climate, soil moisture and soil nutrients, exerts considerable influence on vegetation distribution (e.g., Larsen 1930, Daubenmire 1943, Major 1951, Pojar et al. 1987). It follows, therefore, that a comprehensive ecosystem classification will incorporate vegetation and attributes of the physical environment.

The habitat type and community type concepts are the only “fine-scale” classifications currently available in the central Rocky Mountains. Because they are entirely based on vegetation (Pfister 1976), an explicit link is missing between vegetation and physical environment. An effective organizational structure of terrestrial ecosystems should organize ecosystems hierarchically based on fundamental spatial and functional differences. A comprehensive terrestrial ecosystem classification developed within this hierarchical framework provides that missing link; it integrates three independent classifications: zonal (climatic); vegetation; and site classification (Meidinger and Pojar 1991).

Such a comprehensive ecosystem classification can provide insight into a number of fundamental ecological questions, for example: (1) are there identifiable vegetation-climatic zones as firm altitudinal belts (Daubenmire 1943) in the study area and in the central Rocky Mountains? (2) What are vegetation patterns and important species assemblages in the study area? (3) In addition to climate, what are the environmental factors associated with the distribution of vegetation in the study area and in the central Rocky Mountains? (4) Is it possible to detect ecosystem dynamics i.e., disturbance history and successional trends based on physical environment? These and other insights have important implications for ecosystem science, outreach, education, and management (e.g., Kotar 1988, Bailey 2006, Sharik et al. 2010).

In this dissertation, a mountaineous study area in northern Utah was selected as representative of a general area of the Rocky Mountains. General goals were: (1) to construct three independent classifications: zonal (climatic); vegetation; and site classification; and (2) integrate these classifications into a comprehensive terrestrial ecosystem classification based on an ecosystem hierarchical framework.

The framework of ecosystem hierarchical organization (the levels L+1, L, and L-1) is introduced in Chapter 2. It explains ecosystem complexity using a bottom-up and top-down approach. Using multivariate ordination, environmental gradients are found and then used to construct ecosystem organizational hierarchy.

Broad vegetation-environmental relationships based on understanding of ecosystem organization, particularly at the highest level L+1, are introduced in Chapter 3. Vegetation patterns together with important environmental factors operating at the L+1 level were assessed in zonal context and zonal (climatic) structure was suggested.

In Chapter 4, units of existing vegetation were identified independently of the physical environment. A more objective and statistical approach using fidelity and diagnostic species concept was applied to vegetation classification.

Site classification revealed important environmental factors at the levels L and L-1 in Chapter 5. This classification was overlayed with independent vegetation classification to detect relationship between physical environment and existing vegetation, resulting in comprehensive ecosystem classification for 136 sample plots within subalpine climatic zone.

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CHAPTER 2

ORGANIZATION OF TERRESTRIAL ECOSYSTEMS IN THE ROCKY MOUNTAINS, NORTHERN UTAH [1]

Abstract

Currently, there is no comprehensive terrestrial ecosystem classification for the central Rocky Mountains of the United States. Fundamentals of direct gradient analysis and spatial hierarchy theory were used to develop an organizational structure of terrestrial ecosystems in a mountainous study area in northern Utah.

This structure was derived from intensive sampling of both forest (spruce-fir, Douglas-fir, aspen, juniper and mahogany woodland) and non-forested (willow-riparian, shrublands, tall-forb meadows and grasslands) ecosystems. One-hundred and sixty-three plots were described by physiographic features and soil properties such as nutrient pools and dynamics. The SNOwpack TELemetry and the National Weather Service Cooperative Observer Program weather station network were used to approximate climate of sample plots. A complex dataset of environmental variables was analyzed using ordination.

Ecologically meaningful gradients accounted for 54% of the total variance in the environmental data. Within the large environmental diversity in the study area three levels of ecosystem organization were distinguished: (1) macroclimatic; (2) mesoclimatic, accounting for local climate and moisture distribution; and (3) edaphic -

[1] Coauthored by Antonin Kusbach, Helga Van Miegroet, and James N. Long

soil fertility. The climatic data were used to document the importance and dominant role of macroclimate.

The proposed structure is consistent with the recent USDA, Forest Service ECOMAP and Terrestrial Ecological Unit Inventory approach and will serve as a conceptual framework for a comprehensive ecosystem classification.

Introduction

Rocky Mountain ecosystems are diverse in terms of vegetation as well as climate, topography, geology, and disturbances. Understanding these ecosystems requires classification accounting for the underlying complexity in important environmental drivers. Because the multi-scale character of these drivers results in multi-scale ecosystem patterns (Bailey 2002, O'Neill 2005, Wu 2007) development of such a classification requires a conceptual framework based on a meaningful hierarchical organization (e.g., O'Neill et al. 1986, King 1997, 2005, Wu 2007).

There are three dimensions of scale with which to characterize natural elements or events: (1) time; (2) space; and (3) organizational hierarchy (Wu 2007). Time and space have been frequently used as scalers in ecological studies; however, until recently, hierarchical system organization has received little attention in landscape ecology (King 1997, Wu 2007). For example, landscape classifications throughout Western North America have been based almost entirely on spatial scale (Merriam 1890, Daubenmire 1943, Krajina 1965, Küchler 1969, Omernik 1987, Viereck et al. 1992). While space and time are quantifiable (e.g., area in square meters, time in years), organizational hierarchy, as a directional ordering of interacting entities with distinctive process rates, is qualitative

(Wu 2007). Organizational hierarchy is represented by levels, and because ecosystems exist in space and time, levels always correspond to spatial and temporal scales (Wu 2007). Levels are definitional, and typically organized using a triadic structure in which the focal level “L” is between the next lower level “L-1”, and the next higher level “L+1” (O’Neill 1989, Bissonette 1997, King 1997).

The focal level (L) is chosen by the investigator as the level of interest (Allen et al. 1984, O’Neill 1989). It might, for example, represent tissues in a conventional biological system (King 1997). The next lower level (L-1) represents cells making up tissues; the next higher level (L+1) represents organs. In this hierarchical structure, mechanistic or quantitative understanding of the tissue level (L) can be found at the cell level (L-1) because tissue consists of elements (cells) of the lower level (Beckner 1974, O’Neill et al. 1986, Bissonette 1997). But we cannot explain tissue function just by looking at cells (from the bottom-up). We also need a top-down view; to know a tissue’s biological role requires the context of the next higher level (L+1) represented by organs inside an organism (O’Neill et al. 1986, Urban et al. 1987, King 1997). Similarly in landscape ecology, systems are too complex to be explained just from the bottom-up by mechanistic addition (O’Neill and King 1998, Turner et al. 2001, King 2005). Rather, both bottom-up and top-down approaches are necessary to account for complexity of ecosystems (Rowe and Barnes 1994, Chen et al. 2008).

Life or vegetation zones were the foundation of the earliest ecological land classifications in the Rocky Mountains (Merriam 1890, Shreve 1915, Daubenmire 1943). In this approach, the zones are characterized by major plant species (Whittaker 1972, Long 1994). Life zones provide a useful overview of vegetation pattern across large geographic areas (thousands of km^2) such as San Francisco Peaks, Arizona (Fig. 2.1a, b); however, these zones are too broad to capture important details of vegetation pattern along complex environmental gradients such as elevation, topography, and soils (Fig. 2.1c) (Daubenmire 1943). Peet's (2000) vegetation zonation, based on Whittaker and Niering (1965), incorporates topographical features as a potential second level of organization and makes explicit the influence of elevation and topography-moisture gradients on vegetation zonation. While it is an enhancement on simple life zones (altitudinal belts *sensu* Merriam) this two-level approach to vegetation zonation still does not completely capture important details of ecosystem complexity.

Climate, soil moisture, and soil nutrients are generally believed to be fundamental environmental factors influencing the distribution of vegetation and have been frequently invoked in ecosystem classifications (e.g., Pogrebnyak 1930, Hills 1952, Krajina 1965, Pojar et al. 1987, Meidinger and Pojar 1991). We used direct gradient analysis and spatial hierarchy theory (in the form of a triadic structure) to explicitly assess the roles of the physical environment (Pojar et al. 1987) in the distribution of vegetation within a complex landscape typical of the central Rocky Mountains to improve our conceptualization of these semi-arid ecosystems.

Our overarching goal is to develop a conceptual framework, based on hierarchical organization, for ecosystem classification of the northern Wasatch Range. Our specific objectives are: (1) to determine the important environmental gradients influencing ecosystem patterns; and (2) use these gradients to characterize ecologically meaningful levels of ecosystem organization.

Methods

Study area

Franklin Basin (FB) is a montane-subalpine area, approximately 15,000 ha in size, situated between the Bear River Range and the Wasatch Range in the central Rocky Mountains on the Utah and Idaho border. Smaller in size (ca 1000 ha), the T.W. Daniel Experimental Forest (TWDEF) is situated on the high ridge plateau of the Wasatch Range (10 km to the southeast of FB). Logan Canyon is lower in elevation and together with FB and TWDEF makes up the study area (ca 20,000 ha, and ca 1,400 m of vertical extent) (Fig. 2.2).

According to Bailey (1998a) and McNab et al. (2007), the study area occurs within M331 Southern Rocky Mountains Steppe-Open Woodland-Coniferous Forest-Alpine Meadow Province, “D” Overthrust Mountain Section, “n” Northern Wasatch Range, and “o” Bear River Front Range Subsections. The mean total annual precipitation ranges from about 720 to 1250 mm and mean annual air temperature ranges from 2.4 to 5.7 ^{o}C for Temple Fork, Tony Grove Lake, Franklin Basin, and Utah State University (USU) Doc Daniel weather stations (http://www.wcc.nrcs.usda.gov/snow/).

According to Köppen’s climatic classification modified by Trewartha (1968), the study area is characterized by the microthermal/cold snowy-forest climate; while the lower portion occurs in the cool temperate climate, and the highest portion of the study area occurs in the subalpine-boreal climatic type.

The terrain is mountainous, rocky and steep with occasional flat to gently sloping high ridge-plateaus and benches. The elevation ranges from 1590-3060 m across the three study sites. The highest area of the Bear River Range was glaciated during the

Pleistocene as manifested by glacial geomorphologic features like moraines, U-shaped valleys, erratics, and irregular glacial deposits (Young 1939, Degraff 1976). The study area is mostly built from calcareous sedimentary rocks (limestone, dolomite) with inter-layered quartzite, and from Tertiary sediments consisting of grit, conglomerate, and siltstone of the Wasatch Formation at the TWDEF. The soils are formed in residuum, colluvium, alluvium, glacial till and outwash, and occur on diverse landforms such as cliffs, talus slope, moraines, karst valleys, mountain slopes, landslides, plains, valleys, depressions, ravines, and wetlands (Schoeneberger et al. 2002).

Over half of the study area is occupied by forest ecosystems including Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*); woodland ecosystems including mountain mahogany (*Cercocarpus ledifolius*) and Rocky Mountain juniper (*Juniperus scopulorum*); and riparian, mostly willow (*Salix spp.*) ecosystems. Areal extent and basic types of forest ecosystems are very similar to those of the mid-1800s at the beginning of European settlement. Substantial changes in fire regimes, often in combination with cutting and grazing, have led to dramatic changes in the structure and the age-class distribution of forest stands. In many places, 100- to 140-year-old stands are now predominant (Long 1994). Forests in the study area are thus characterized by mid- and late-seral stages where potential climax tree species are easily recognizable and forest understory is usually well developed (Pfister and Arno 1980). Non-forested ecosystems include willow-riparian communities, shrublands (*Artemisia spp.*), meadows and grasslands, which may represent stable or temporary communities. Despite human impacts in last 120 years, the study area is considered as relatively natural in terms of plant species composition (Bird 1964).

Data collection

Sampling was intensive enough to capture as much ecosystem variation as possible focusing on all major existing plant communities (Brohman and Bryant 2005) occupying all major landforms (Schoeneberger et al. 2002), but avoiding ecotones and recently disturbed (burned, logged, damaged by insects) areas. One-hundred-sixty-three sample plots were established within the study area in the summers of 2006 and 2007. A stratified (based on vegetation physiognomy) fixed (subjective selection) sampling design was used with sample plot size of 1000 m^2 for forest and 100 m^2 for non-forested ecosystems (Brohman and Bryant 2005). Three replicate plots were considered the minimum for defining a vegetation unit. We anticipated 50-60 units based on a preliminary reconnaissance of the study area. To distinguish among units, we followed recommendations of Grossman et al. (1998).

As the study focused on environmental gradients; we did not examine historical gradients and biotic interactions (e.g., plant competition, allelopathy, mycorrhizae). To characterize the environmental gradients we described each sample plot in terms of relatively static or constant attributes i.e., physiographic variables such as elevation, slope aspect, slope gradient, topographic position, and slope shape (Lotspeich 1980); dynamic attributes such as O and A horizon thickness, humus form, pH, nutrient pools characterizing relatively slow processes; and attributes such as nutrient supply rates describing relatively fast processes (Table 2.1). One soil pit was dug in each sample plot to the unweathered parent material or permanent water table. Description and sampling of pedons followed practices and terminology of the National Cooperative Soil Survey (Soil Survey Staff 1999, 2006, Schoeneberger et al. 2002). Humus form was identified following Green et al. (1993).

One composite soil sample from 0-30 cm was collected from a pedon face in each plot, air dried and sieved (< 2 mm), and the fine fraction analyzed for texture classes (sandy, loamy, clayey) using the feel-method (Thien 1979), for pH (1:1 soil in water) using a Corning pH analyzer, and $CaCO_3$ content by treating the samples with HCl using a mercury manometer (Loeppert and Suarez 1996). The total C and N concentration were determined by dry combustion using a LECO CN analyzer (LECO TrueSpec C/N, Leco Corp., St. Joseph, MI). A static-absolute nutrient availability index (SNAI), i.e., cation pool “snapshot”, was determined by extracting exchangeable cations with 1 M HN_4Cl at pH 7.0 using a mechanical vacuum extractor (Holmgren et al. 1977) and cation analysis of extractant using an inductively coupled plasma spectrophotometer (ICP) (Iris Advantage, Thermo Electron, Madison, WI). Extractable P (PO_4) was determined by the Olsen P method (Olsen et al. 1954) using sodium bicarbonate extraction, followed by P analysis using Thermo Electron Spectronic 20 Genesys spectrophotometer. Total mineralizable nitrogen was determined from 7-day anaerobic incubation and extraction with 2 M KCl (Keeney and Bremmer 1966) followed by NH_4 analysis (Lachat Quickchem 8000, Flow Injection Analyzer).

To determine a dynamic-relative nutrient availability index (DNAI) (Qian and Schoenau 2002), plant root simulators (PRS™-probes; Western Ag Innovations, Inc., Saskatoon, Canada), a combination of anion and cation exchange membranes, were buried vertically into the mineral soil at each site for 6 weeks (during September and November). PRS™-probes were cleaned and sent to Western Ag Innovations for extraction and chemical analysis including Ca, Mg, K, S, Fe, Mn, Zn, Cu, Pb, Al, NH_4 cations, and NO_3 and PO_4 anions (Table 2.1). One of 163 exchange membrane sets was not recovered.

Climatic data such as air temperature, precipitation, soil temperature (depth of 50 cm), and soil moisture (depth of 20 cm and 50 cm) for the northern Wasatch Range (corresponding with M331D Section in McNab et al. (2007)) were obtained from nearby weather stations to approximate ambient and soil climate of the sample plots. Both, the Natural Resources Conservation Service (NRCS) SNOwpack TELemetry (SNOTEL; http://www.wcc.nrcs.usda.gov/snow/) and the National Weather Service Cooperative Observer Program (COOP; http://www.nws.noaa.gov/om/coop/) station networks provide long term observations for air temperatures and precipitation (>10 years). Soil temperature and moisture at SNOTEL sites were available for 6 years (2003-2008) and there were two COOP stations with soil temperature measurements for the northern Wasatch Range. Accuracy of the analysis may therefore be limited by the short data record. Nevertheless, these data were an important source of information in this analysis.

Data analysis

We used direct gradient analysis (e.g., Whittaker 1973, Austin et al. 1984) to order the sample plots according to environmental attributes (McCune and Grace 2002).

We analyzed a dataset consisting of 163 sample plots and 43 variables. Because of the complex environmental character of the dataset we used Principal components analysis (PCA) (Pearson 1901) in order to: (1) reduce dimensionality of the dataset, i.e. to represent a large dataset with a smaller number of composite variables; (2) assess the composite variables as significant principal components (PCs); and (3) interpret the significant PCs as environmental gradients (McCune and Grace 2002). Orthogonal rotations and correlation type of a cross-products matrix were used to get independent, mutually uncorrelated PCs (Lattin et al. 2003).

Slope aspect, measured in azimuth degrees and corrected for magnetic declination, was converted from a circular to a linear form representing "coolness" (Roberts and Cooper 1989). The maximum aspect value (*av* = 1.0, the coolest conditions) occurs at 30 degrees aspect, and the minimum (*av* = 0.0, the warmest conditions) at 210 degrees aspect. We transformed the variables with $|\text{skewness}|>1$ to be close to multivariate normality, standardized the data by adjustment to standard deviate (*z*-scores), and checked the dataset for outliers using a cutoff of 2.0 standard deviations from the grand mean (McCune and Grace 2002).

Significance of PCs was tested by a graphical approach (Cattell 1966) and Monte Carlo randomization test (McCune and Mefford 2006). We calculated correlation coefficients (loadings) with each ordination axis, the linear (parametric Pearson's *r*) and rank (nonparametric Kendall's *tau*) relationships between the ordination scores and the observed variables. Our use of *r* and *tau* is suggested to be, even in relatively small datasets, more conservative than *p*-values for the null hypothesis of no relationship between ordination scores and variables (McCune and Grace 2002). We set the threshold for *r* and *tau* > 0.35.

Additionally, linear regressions were used to assess: (1) the role of elevation in the PCs; (2) the relationship of climatic variables with elevation; (3) the relationship of soil moisture with elevation and precipitation; and (4) the relationship of understory vegetation cover with soil development represented by soil depth, coarse rock fragments content, and A horizon thickness. The variables were transformed for normality by power or logarithmic transformation when necessary.

R software, ver. 2. 7. 2. (http://www.r-project.org/) and PC-ORD (McCune and Mefford 2006) were used in the analysis.

Results

Principal components analysis was run three times; the first run was based on the entire original dataset (163 sample plots, 43 variables). The second PCA was run on the reduced dataset (163 sample plots, 5 variables) retaining only the physiographic variables (elevation, topographic position, slope gradient, slope aspect, and slope shape). Assuming that elevation is a surrogate for the highest level of organizational hierarchy (L+1 level in the triadic structure) and may affect additional analysis of the lower levels (L and L-1), we dropped it from the original dataset in the third PCA run.

In the first PCA run, Cattell's approach with a pronounced elbow just after the fifth PC and variances of remaining PCs (proportions ≤ 4% for each) declining approximately linearly, suggested five statistically significant PCs (Fig. 2.3). Also the Monte Carlo test with 5000 randomizations showed significant *p*-values for the first five PCs (Table 2.2).

Elevation was the only physiographic variable whose loadings were significant and stable i.e., they did not fluctuate highly for the four significant PCs (e.g., max. r = 0.40

for PC1 and min. $r = 0.28$ for PC2, PC4; and max. *tau* = 0.28 for PC1 and min. *tau* = 0.20 for PC2) in contrast with e.g., topographic position where loadings ranged from $r = 0.78$ for PC2 to $r = 0.07$ for PC3, PC4 (Table 2.3). Multiple regression also demonstrated a relationship between elevation and the first four PCs ($F = 4.98$, $R^2 = 0.52$, PC1 - PC4: $p < 0.001$).

The second PCA run provided physiographic insight. A single significant principal component (PC1 as the axis 1) accounted for 45% of the total variance (Table 2.2). A joint plot (Fig. 2.4), a diagram of radiating lines (vectors), indicated strength (vector length) and direction (vector angle) of relationships of the variables with ordination axes (McCune and Grace 2002). Topographic position, slope gradient, and slope shape together reflected strong topographical/morphometric meaning of the axis 1. Elevation had a weaker but nevertheless important influence on this axis (Table 2.3).

General importance of elevation was also documented by regressions with the climatic data. Elevation is a predictor for mean annual air temperature (MAAT: $p < 0.001$, $R^2 = 0.67$), mean total annual precipitation (MTAP: $p < 0.001$, $R^2 = 0.39$), and soil temperatures (mean annual, MAST: $p < 0.001$, $R^2 = 0.61$; mean summer, MSST: $p < 0.001$, $R^2 = 0.43$). Mean winter soil temperature (MWST) was poorly correlated with elevation ($p < 0.8$, $R^2 = -0.03$) most likely because of snowpack insulation (Fig. 2.5a, b). Soil moisture at 20 and 50 cm depths was little affected either by elevation or precipitation (Fig. 2.5c, d).

To gain ecological insight into the lower hierarchical levels (L and L-1) and discriminate among them, we reran PCA without elevation. In this third PCA run (163 sample plots, 42 variables), five statistically significant PCs accounted for 60% of the total variance in the dataset (Table 2.2). We thus reduced 42 variables to five statistically significant PCs, thereby reducing dimensionality of the problem by 88%. When comparing the first and third PCA runs, we obtained the same number of statistically significant PCs but the numerical summary was better for the third PCA run (Table 2.2). There were also differences among loadings between the first and third PCA runs (e.g., pH, NO_3 DNAI, Fe and Mn SNAI, Table 2.3). Because of improved results, the third PCA run was used for the interpretation of principal components.

In our analysis the first two PCs or gradients (collectively explaining 35% of the variance in the dataset) might not be adequate to explain the complex environment. On the other hand, there is the risk of interpretation of weak patterns with more dimensions (McCune and Grace 2002). The fifth PC, despite its statistical significance, is not readily interpretable as there are just five significant loadings for this PC (Table 2.3). Therefore, instead of five statistically significant PCs, we interpreted four ecologically meaningful PCs (Fig. 2.3). Based on significance of the loadings, the first principal component (PC1) was associated with parent material and soil properties (soil color, pH, $CaCO_3$ content); total N and C; Ca, Mg and K DNAIs; and N, Ca, Mg and metals SNAIs (Table 2.3). We interpreted PC1 as an indicator of **soil fertility**, differentiating between rich (sufficiency of macronutrients) and poor (deficiency of macronutrients) ecosystems.

The second principal component (PC2) was related to topographic position, slope gradient, slope shape with soil properties (soil depth, coarse rock fragment content, $CaCO_3$ content) affecting soil moisture conditions (indicated by water table and mottles). It was interpreted as **local topography** accounting for soil moisture. Because we did not measure soil moisture directly we did not consider it as an explicit environmental gradient. The interpretation was consistent with interpretation of PC1 in the second PCA run. PC2 generally differentiates between "caplands" and "cuplands" (Devlin et al. undated), and steepness and gentleness of the terrain. For instance, one may find completely different plant communities within a short distance (e.g., meters) where a moist, concave pocket of aspen changes abruptly into a dry, rocky, convex island of mountain mahogany.

The third principal component (PC3) was associated with soil organic matter (SOM) (O and A horizon thickness, humus form), mineralizable N DNAI, NO_3 and NH_4 DNAIs (Table 2.3). We interpreted this PC as indicative of **microbial activity**, influencing SOM decomposition rate. This rate is conditioned by overall climate (as represented by elevation in the first PCA run), and expressed by surface soil horizon properties (O and A horizon thickness, humus form) as well as by indicators of N availability. It influences the nutrient/chemical environment by either NH_4 mineralization or nitrification.

The last interpretable principal component (PC4) was associated with coarse rock fragment content and soil depth, with DNAIs of mobile nutrients (N, S) and relatively immobile metals (Fe, Mn, Zn), and K SNAI. It was interpreted as **soil development**, reflecting the amount of parent material residuum (soil "rockiness") and soil permeability. More developed and older soils are deeper, contain less coarse rock fragments. These soils have high total porosity and high water holding capacity because water movement in soil micropores is slow. In contrast, less developed soils are younger and shallower, and contain high amounts of coarse rock fragments. These soils have low total porosity but high macroporosity, resulting in low water holding capacity, but fast water infiltration and percolation via macropores. Rapid water flow in these soils creates pulses of plant-available nutrients in soil solution.

These less developed soils, on the other hand, had less understory vegetation cover. The high DNAIs for N, S and metals captured by PRS™-probes combined with low nutrient uptake potential associated with low understory vegetation cover, thus imply possible greater nutrient leaching loss from less developed, young, skeletal soils.

Discussion

Development of a hierarchical organization from the complex dataset represented a compromise between complexity, understandability, and applicability. We synthesized functionally similar principal components to environmental gradients and used them as the definitional levels of ecosystem organization (Table 2.4).

That elevation is strongly associated with climate has long been observed (e.g., Merriam 1890, Larsen 1930, Daubenmire 1943). Our data revealed that elevation: (1) is superimposed over all the meaningful principal components; (2) differs from the other physiographic variables, which have topographical or morphometric meaning (Lotspeich 1980); and (3) is strongly correlated with climate. Therefore, we consider elevation an appropriate surrogate for **regional climate** as the macroclimatic level (Major 1951, Bailey 2002).

Analyzed importance of elevation was consistent with altitudinal zonation of mountains (e.g., Krajina 1965, Bailey 1998a, b). In mountains, ecosystems change with elevation because of the change of climate; the use of the term regional climate/macroclimate in an elevation sense is therefore appropriate. Elevation or macroclimatic zones should be seen as relatively narrow vertically stacked belts with abrupt climatic transition rather than gradual changes over vast horizontally extended areas.

The other physiographic variables, topographic position, slope gradient and slope shape were significant predictors of PC2 (local topography). This gradient was an important local topo-climatic attribute because it is modified by local topography (Major 1951, Thornthwaite 1954) finally accounting for soil moisture conditions. We considered it a surrogate for **local climate** as the mesoclimatic level (Major 1951).

Soil properties were significant predictors of PC1, PC3 and PC4. Because of the orthogonality of ordination axes, soil fertility was not correlated with soil development as well as with microbial activity. However, these gradients were in fact functionally similar in their impact on plant nutrition; they affect presence or absence of plant-available nutrients. We considered them a surrogate for **soil fertility** as the edaphic level.

We differentiated among the levels of ecosystem organization: regional climate (L+1); local climate (the focal level, L); and soil fertility (L-1). We superimposed local climate over fertility because of their cause-effect relationship; soils are more dynamic (i.e., they are “faster”) and act at a finer temporal and spatial scale (Urban et al. 1987, King 1997). At the focal level, ecosystems are affected by meso- or local climate. Ecosystems in the context of the level L-1 are differentiated by fertility and together with the focal level ecosystems they build up the L+1 level (bottom-up/inductive approach). To understand these lower level (L, L-1) ecosystems, they must also be placed in the context of macroclimate (L+1) (top-down/deductive approach).

For example, the Engelmann spruce-subalpine fir (S-F) zone stretches across the levels L+1, L, and L-1 (Fig. 2.6). The ecosystem organization enabled stratification of this extremely environmentally diverse S-F zone. We know now that poor and fertile S-F communities from the fertility level (L-1) can be found in different conditions of the local climate (L) (e.g., on warm/dry vs. cool/moist slopes or valleys). As a result, S-F communities appear in very different elevations and local climates because of the compensating effects of environmental factors on plants (Pojar et al. 1987). Thus, S-F communities occur as a high-elevation regional ecosystem (Klinka and Chourmouzis 1999, K. Klinka 2009, personal communication); however, they may also occur in lower elevations because local environmental conditions modify the influence of low-elevation regional climate (Major 1969). For example, S-F communities descend on cool shady slopes or as riparian/wetland communities along valley bottoms (Fig. 2.1c).

Our hierarchical ecosystem organization corresponds well to lower elements of the Hierarchical Framework of Ecological Units (Cleland et al. 1997, ECOMAP 2007) and the Terrestrial Ecological Unit Inventory (TEUI) Technical Guide (Winthers et al. 2005). Regional climate represented by elevation matches landscape and even subregion, local climate and soil fertility match land unit of the ECOMAP/TEUI standard (Table 2.4).

We made no *a priori* assumptions about environmental factors associated with the various levels in our organizational structure. Rather, the apparent roles of climate, topography, and soil nutrients within the landscape hierarchy were derived from the data (O’Neill and King 1998).

We anticipate the organizational structure will contribute to implementation of spatial hierarchy theory (O’Neill 2005) to the practice of classification as well as to its application into ecosystem management (e.g., by landscape managers or foresters) (Sharik et al. 2010).

Summary and conclusions

We found ordination to be a valuable technique to organize ecosystems and detect multiple scales of pattern based on interpretation of the meaningful principal components. By using PCA we were able to confirm the environmental heterogeneity of the study area, derive important environmental gradients influencing ecosystem patterns within that area, and synthesize these gradients into ecologically meaningful levels of ecosystem organization. These are: (1) macroclimate as the level L+1; (2) mesoclimate as the focal level (L); and (3) soil fertility as the level L-1.

Our hierarchical ecosystem organization represents an improvement on earlier land classifications in the Rocky Mountains by adding another dimension. This structure is consistent with the lower elements of the ECOMAP/TEUI standard.

We conclude that this organization can be used as a framework for additional structuring e.g., site (ecotope, habitat) classification. We intend to use this hierarchy in building a comprehensive ecosystem classification system that will serve as a tool not only for communication in ecosystem research but also for practical ecosystem management.

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Table 2.1. Research variables. Dynamic nutrient availability index (DNAI) indicated by '*d*', static nutrient availability index (SNAI) indicated by '*s*' in abbreviations. NA-not applicable.

Variable	**Abbreviation**	**Units/Values**
Elevation	elev	meters
Topographic position	topos	1-crest,shoulder, 2-back slope, 3-foot slope, 4-flat (<5%), 5-toeslope, 6-depression
Slope gradient	sl	%
Slope aspect	av	aspect values 0-1 (Roberts and Cooper 1989)
Slope shape	shape	1-convex, 2-linear, 3-concave
Parent material	parmat	1-quartzite, 2-Wasatch Formation, 3-till, 4-limestone or dolomite, 5-colluvium, 6-alluvium
Soil O-horizon depth	Ohor	centimeters
Soil A horizon depth	Ahor	centimeters
Humus form	hum	values 1-17; e.g., 1-fibrimor, 10-mormoder, 14-rhizomull, 17-no humus (Green et al. 1993)
Soil depth	sdepth	centimeters
Coarse rock fragment content	RF	% volumetric
Soil water table	wtable	1- up to 30cm depth, 2- 30-80cm, 3- 80-150cm, 4- no water table
Soil mottles	mottles	1- up to 30cm depth, 2- 30-80cm, 3- 80-150cm, 4- no mottles
Soil color value	cvalue	1-7 according to Munsell® notation
Soil texture	text	1-sandy, 2-loamy, 3-clayey
Soil pH	pH	1-14 pH scale
Calcium carbonate content	$CaCO_3$	%
Total nitrogen	Nox	%
Total carbon	Cox	%
Carbon nitrogen ratio	C.N	NA
Mineralizable nitrogen DNAI	Nmin_d	microgram/10 cm^2/6weeks
Nitrate DNAI	NO3_d	microgram/10 cm^2/6weeks

Ammonium DNAI	NH4_d	microgram/10 cm^2/6weeks
Calcium DNAI	Ca_d	microgram/10 cm^2/6weeks
Magnesium DNAI	Mg_d	microgram/10 cm^2/6weeks
Potassium DNAI	K_d	microgram/10 cm^2/6weeks
Phosphorus DNAI	P_d	microgram/10 cm^2/6weeks
Iron DNAI	Fe_d	microgram/10 cm^2/6weeks
Manganese DNAI	Mn_d	microgram/10 cm^2/6weeks
Zinc DNAI	Zn_d	microgram/10 cm^2/6weeks
Sulphur DNAI	S_d	microgram/10 cm^2/6weeks
Aluminum DNAI	Al_d	microgram/10 cm^2/6weeks
Mineralizable nitrogen SNAI	Nmin_s	milligram/kilogram
Ammonium SNAI	NH4_s	milligram/kilogram
Calcium SNAI	Ca_s	milligram/kilogram
Magnesium SNAI	Mg_s	milligram/kilogram
Potassium SNAI	K_s	milligram/kilogram
Phosphorus SNAI	P_s	milligram/kilogram
Iron SNAI	Fe_s	milligram/kilogram
Manganese SNAI	Mn_s	milligram/kilogram
Zinc SNAI	Zn_s	milligram/kilogram
Sulphur SNAI	S_s	milligram/kilogram
Aluminum SNAI	Al_s	milligram/kilogram

Table 2.2. PCA summary for ten principal components. Ecologically meaningful PCs are in bold.

1st run	**PC1**	**PC2**	**PC3**	**PC4**	PC5	PC6	PC7	PC8	PC9	PC10
Eigenvalue	**8.18**	**6.88**	**4.78**	**3.2170**	2.33	1.60	1.53	1.23	1.20	1.16
% of Variance	**19.03**	**15.99**	**11.11**	**7.48**	5.41	3.73	3.56	2.87	2.78	2.71
Cumulative % of Var.	**19.03**	**35.02**	**46.13**	**53.61**	59.03	62.75	66.31	69.17	71.96	74.66
p- value	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0002	0.9832	0.9926	1.0000	1.0000	1.0000
3nd run										
Eigenvalue	**8.05**	**6.80**	**4.66**	**3.15**	2.33	1.54	1.48	1.23	1.19	1.15
% of Variance	**19.17**	**16.20**	**11.10**	**7.49**	5.54	3.66	3.52	2.93	2.82	2.74
Cumulative % of Var.	**19.17**	**35.37**	**46.47**	**53.96**	59.50	63.16	66.68	69.61	72.43	75.17
p- value	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0002	1.0000	1.0000	1.0000	1.0000	1.0000
2nd run										
Eigenvalue	**2.26**	1.15	0.68	0.61	0.30					
% of Variance	**45.14**	23.05	13.64	12.16	6.01					
Cumulative % of Var.	**45.14**	68.19	81.83	93.99	100.00					
p- value	**0.0002**	0.0804	1.0000	1.0000	1.0000					

Table 2.3. PCA loadings. Significant Pearson's (*r*), and Kendall's (*tau*) coefficients are in bold. Both significant *r* and *tau* express a significant variable for the particular PC (shaded). Variables are defined in Table 2.1. NA - not applicable.

	PCA first run								PCA third run								PCA second run	
Variable	**PC1**		**PC2**		**PC3**		**PC4**	**PC5**	**PC1**		**PC2**		**PC3**		**PC4**	**PC5**	**PC1**	
	r	**tau**	**r**	**tau**	**r**	**tau**	**r**	**r**	**r**	**tau**	**r**	**tau**	**r**	**tau**	**r**	**r**	**r**	**tau**
elev	**-0.40**	**-0.28**[a]	**0.28**[a]	**0.20**[a]	**0.36**	**0.25**[a]	**-0.28**[a]	-0.01	NA	NA	NA	NA	NA	NA	NA	NA	**0.48**	**0.36**
topos	0.20	0.10	**-0.78**	**-0.62**	0.07	-0.05	0.07	-0.36	0.14	0.04	**-0.79**	**-0.63**	0.03	-0.05	0.08	**-0.36**	**-0.89**	**-0.76**
sl	-0.20	-0.03	**0.57**	**0.45**	0.18	0.12	-0.05	0.15	-0.15	0.01	**0.58**	**0.45**	0.21	0.13	-0.08	0.15	**0.75**	**0.54**
av	-0.23	-0.19	-0.16	-0.13	0.29	0.20	0.18	-0.28	-0.23	-0.19	-0.16	-0.13	0.30	0.20	0.16	-0.28	-0.23	-0.15
shape	0.16	0.08	**-0.62**	**-0.50**	-0.02	-0.05	0.23	-0.37	0.11	0.04	**-0.63**	**-0.51**	-0.05	-0.06	0.26	**-0.37**	**-0.79**	**-0.66**
Ohor	0.13	0.09	-0.30	-0.21	**0.75**	**0.42**	0.17	0.16	0.13	0.08	-0.34	-0.23	**0.75**	**0.43**	0.13	0.16		
Ahor	0.27	0.21	-0.21	-0.11	**-0.58**	**-0.45**	0.09	-0.30	0.23	0.19	-0.21	-0.12	**-0.60**	**-0.46**	0.15	-0.30		
hum	-0.05	-0.06	0.25	0.19	**-0.69**	**-0.42**	-0.22	-0.25	-0.05	-0.05	0.27	0.20	**-0.70**	**-0.43**	-0.17	-0.25		
sdepth	0.02	-0.03	**-0.71**	**-0.53**	-0.20	-0.15	**0.36**	-0.20	-0.05	-0.08	**-0.70**	**-0.53**	-0.21	-0.15	**0.39**	-0.20		
RF	-0.26	-0.13	**0.61**	**0.45**	0.18	0.15	**-0.43**	0.30	-0.20	-0.09	**0.62**	**0.46**	0.19	0.14	**-0.46**	0.30		
parmat	**0.63**	**0.41**	-0.33	-0.26	-0.20	-0.16	0.21	-0.20	**0.60**	**0.37**	**-0.36**	-0.28	-0.23	-0.17	0.25	-0.20		
wtable	**-0.36**	-0.20	**0.54**	**0.40**	**-0.42**	-0.24	0.29	0.25	-0.33	-0.18	**0.59**	**0.41**	**-0.37**	-0.22	0.30	0.25		
mottles	-0.31	-0.18	**0.62**	**0.47**	**-0.37**	-0.20	0.23	0.33	-0.28	-0.15	**0.66**	**0.49**	-0.32	-0.17	0.24	0.33		
cvalue	**-0.77**	**-0.63**	-0.12	-0.16	0.02	0.10	0.11	-0.08	**-0.78**	**-0.63**	-0.06	-0.13	0.05	0.11	0.09	-0.08		
text	**0.57**	0.34	-0.23	-0.13	0.05	-0.05	0.23	0.06	**0.54**	0.33	-0.27	-0.15	0.04	-0.03	0.24	0.06		
pH	**0.67**	**0.54**	**0.56**	**0.36**	-0.02	-0.03	0.04	-0.01	**0.70**	**0.57**	**0.51**	0.33	-0.01	-0.03	0.04	-0.01		
CaCO3	**0.38**	**0.43**	**0.64**	**0.57**	0.18	0.12	-0.07	-0.12	**0.43**	**0.48**	**0.60**	**0.55**	0.19	0.12	-0.08	-0.11		
Nmin_d	0.03	0.04	0.19	0.12	**-0.56**	**-0.39**	**-0.63**	-0.08	0.04	0.04	0.20	0.13	**-0.59**	**-0.42**	**-0.60**	-0.08		
Nox	**0.79**	**0.55**	-0.15	-0.05	-0.09	-0.21	-0.11	0.29	**0.77**	**0.52**	-0.21	-0.07	-0.13	-0.22	-0.07	0.29		
NO3_d	0.08	0.08	0.20	0.12	**-0.65**	**-0.45**	**-0.55**	-0.07	0.08	0.08	0.21	0.13	**-0.68**	**-0.47**	**-0.51**	-0.07		
NH4_d	-0.27	-0.18	-0.01	-0.02	**0.39**	0.27[b]	-0.26	-0.10	-0.25	-0.17	-0.01	-0.02	**0.38**	0.26[b]	-0.29	-0.10		

Cox	**0.78**	**0.60**	0.12	0.16	0.17	0.02	-0.07	0.24	**0.80**	**0.63**	0.04	0.13	0.13	0.01	-0.05	0.24
C/N	0.09	0.04	**0.45**	0.24	**0.46**	**0.38**	0.07	-0.10	0.15	0.08	**0.42**	0.22	**0.46**	**0.38**	0.06	-0.10
Ca_d	**0.57**	**0.40**	-0.01	0.01	-0.33	-0.24	-0.18	0.07	**0.56**	**0.38**	-0.04	0.00	**-0.35**	-0.25	-0.17	0.07
Mg_d	**0.51**	**0.36**	0.24	0.11	0.20	0.08	-0.29	-0.26	**0.55**	**0.38**	0.18	0.09	0.17	0.07	-0.28	-0.26
K_d	**-0.55**	**-0.38**	-0.20	-0.22	**-0.43**	-0.23	0.18	0.18	**-0.58**	**-0.41**	-0.14	-0.19	**-0.40**	-0.22	0.19	0.18
P_d	-0.20	-0.17	**-0.39**	-0.29	**-0.47**	-0.34	-0.05	0.26	-0.25	-0.20	**-0.36**	-0.27	**-0.48**	-0.34	-0.02	0.26
Fe_d	0.12	-0.10	**-0.66**	**-0.44**	0.09	-0.09	**-0.54**	-0.03	0.08	-0.13	**-0.68**	**-0.43**	0.03	-0.12	**-0.53**	-0.03
Mn_d	-0.20	-0.23	**-0.51**	-0.32	0.21	0.05	**-0.49**	0.01	-0.23	-0.25	**-0.51**	-0.30	0.18	0.04	**-0.51**	0.00
Zn_d	0.16	0.09	-0.31	-0.15	**-0.36**	-0.27	**-0.55**	0.02	0.13	0.07	-0.31	-0.15	**-0.41**	-0.29	**-0.52**	0.02
S_d	-0.08	-0.12	**-0.45**	-0.27	0.20	0.08	**-0.54**	-0.13	-0.10	-0.13	**-0.46**	-0.26	0.15	0.06	**-0.55**	-0.13
Al_d	-0.11	-0.06	0.14	0.10	-0.25	-0.15	-0.17	-0.15	-0.11	-0.06	0.16	0.11	-0.24	-0.14	-0.18	-0.15
Ca_s	**0.87**	**0.65**	0.04	0.10	0.01	-0.07	0.13	0.28	**0.87**	**0.65**	-0.02	0.07	-0.01	-0.06	0.14	0.28
Mg_s	**0.81**	**0.65**	0.22	0.12	0.29	0.08	-0.02	-0.03	**0.84**	**0.68**	0.14	0.09	0.27	0.08	-0.02	-0.03
K_s	0.25	0.18	-0.19	-0.13	**-0.44**	-0.32	0.37	0.21	0.21	0.15	-0.17	-0.13	**-0.42**	-0.31	**0.38**	0.21
NH4_s	0.31	0.16	**-0.45**	-0.28	0.18	0.06	-0.13	0.34	0.29	0.14	**-0.49**	-0.30	0.14	0.04	-0.11	0.34
Nmin_s	**0.79**	**0.57**	-0.16	-0.02	0.10	-0.06	-0.15	0.25	**0.79**	**0.56**	-0.23	-0.05	0.05	-0.08	-0.12	0.25
P_s	-0.09	-0.13	**-0.43**	-0.33	**-0.38**	-0.31	0.18	**0.41**	-0.14	-0.15	**-0.41**	-0.33	**-0.39**	-0.32	0.22	**0.42**
Al_s	**-0.70**	**-0.55**	-0.24	-0.20	0.25	0.22	-0.07	-0.03	**-0.70**	**-0.56**	-0.20	-0.17	0.26	0.22	-0.09	-0.03
Fe_s	-0.32	-0.24	-0.22	-0.16	**0.43**	0.34	-0.07	0.32	-0.33	-0.25	-0.21	-0.14	**0.44**	**0.35**	-0.12	0.32
S_s	0.23	0.14	**-0.50**	-0.30	0.01	-0.02	-0.16	**0.52**	0.19	0.11	**-0.52**	-0.32	-0.03	-0.04	-0.15	**0.52**
Mn_s	**-0.40**	-0.31	**-0.54**	**-0.43**	-0.04	-0.04	0.01	**0.37**	**-0.44**	**-0.35**	**-0.52**	**-0.42**	-0.06	-0.06	0.04	**0.37**
Zn_s	**-0.47**	**-0.36**	-0.27	-0.20	0.05	0.06	-0.20	0.25	**-0.48**	**-0.37**	-0.25	-0.19	0.03	0.04	-0.19	0.25

[a] significant loadings relatively to *elev* maximum (0.40)

[b] important contrast of ammonium with nitrate nutrient supply rate

Table 2.4. Comparison of USDA Forest Service ecological land classification with ecosystem organization and the environmental gradients.

USDA Forest Service, ECOMAP 2007; TEUI 2005		**Ecosystem organization**	
Scale	Ecological unit	Definitional levels (Environmental gradients)	Environmental principal components
Ecoregion	Domain		
	Division		
	Province		
Subregion	Section	REGIONAL CLIMATE	Elevation
	Subsection		
Landscape	Landtype association		
Land unit	Landtype	LOCAL CLIMATE	Topography
	Landtype phase	SOIL FERTILITY	Soil fertility, soil development, microbial activity

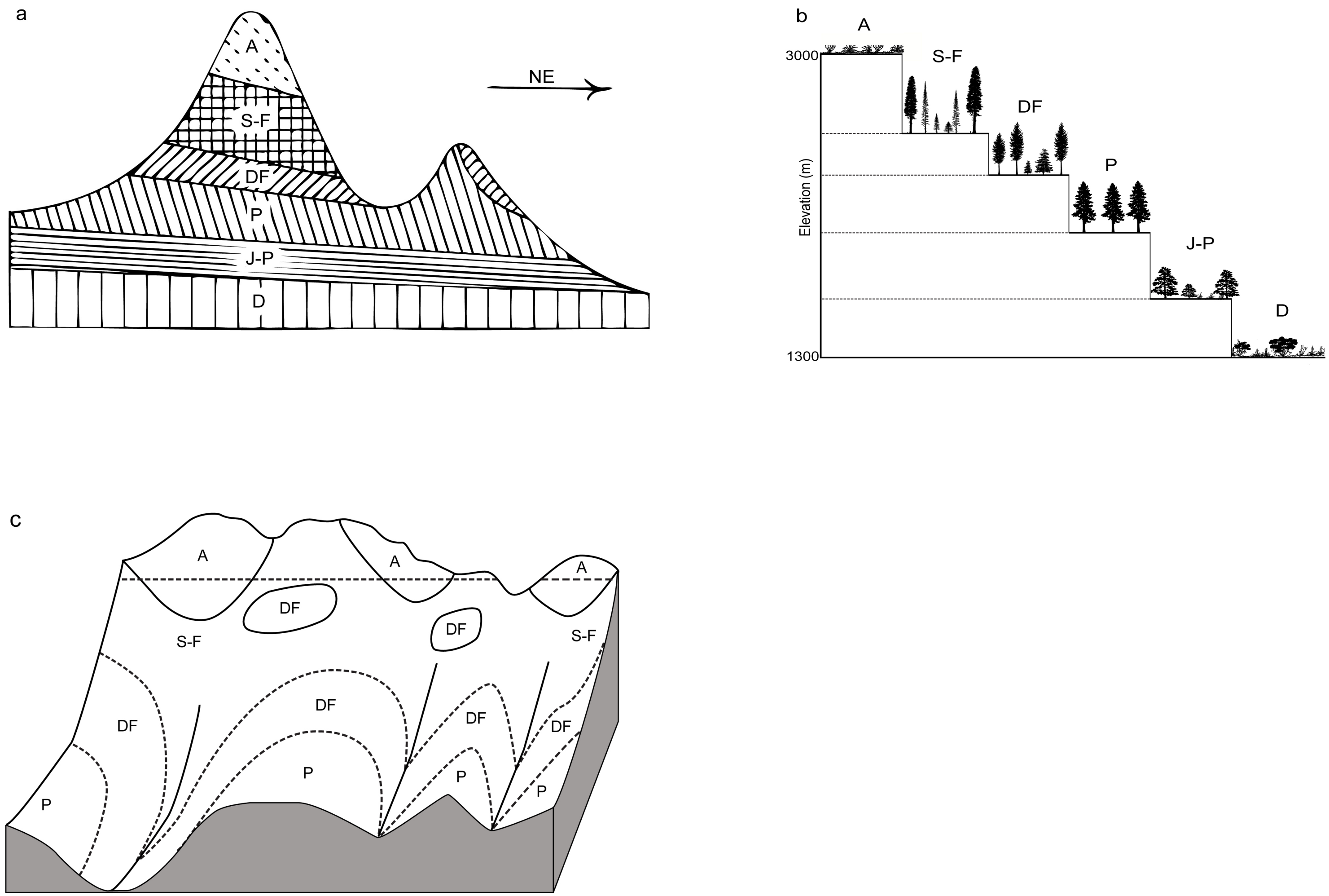
a
A
S-F
DF
P
J-P
D
NE
b
A
3000
S-F
DF
P
J-P
D
1300
Elevation (m)
c
A
A
A
DF
DF
S-F
S-F
DF
DF
DF
DF
DF
P
P
P
P
P

Figure 2.1. Earlier land classifications: (a) life zones as simple elevation belts *sensu* Merriam, (1890) as (b) idealized, stair-like landscape; (c) details of vegetation pattern along complex environmental gradients such as elevation, topography, and soils presented as “telescoping, discontinuity and interfingering” of plant communities leading to inversion of vegetation zones (Daubenmire 1943). Alpine (A), Engelmann spruce-subalpine fir (S-F), Douglas-fir (DF), ponderosa pine (P), juniper-pinyon (J-P), desert (D)

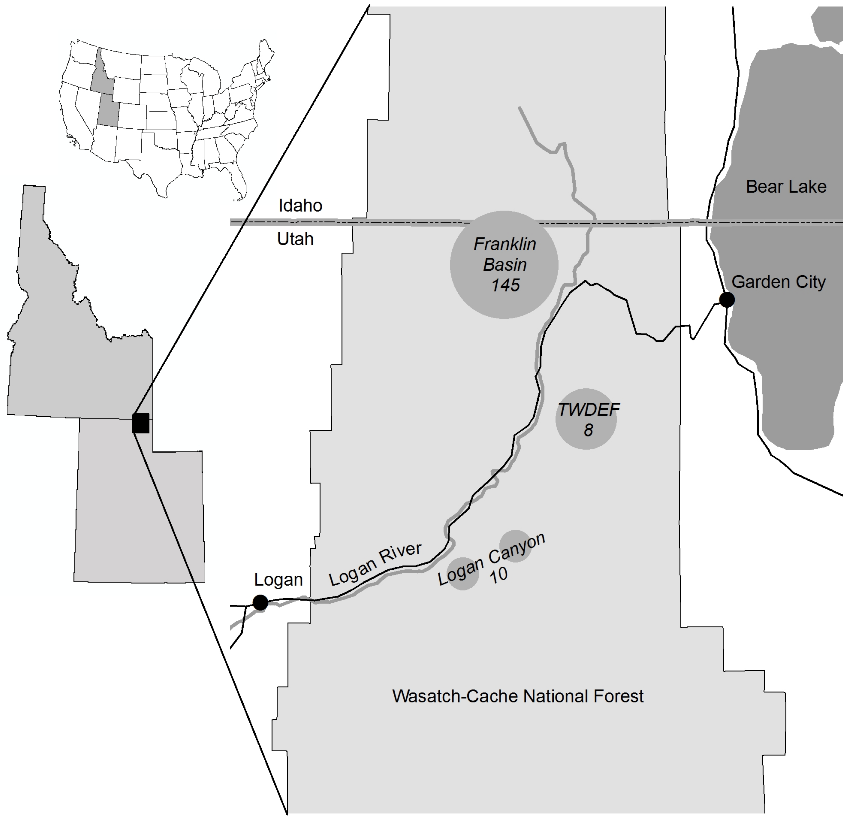

Figure 2.2. The study area on the Utah-Idaho border with subareas; digits represent numbers of the sample plots.

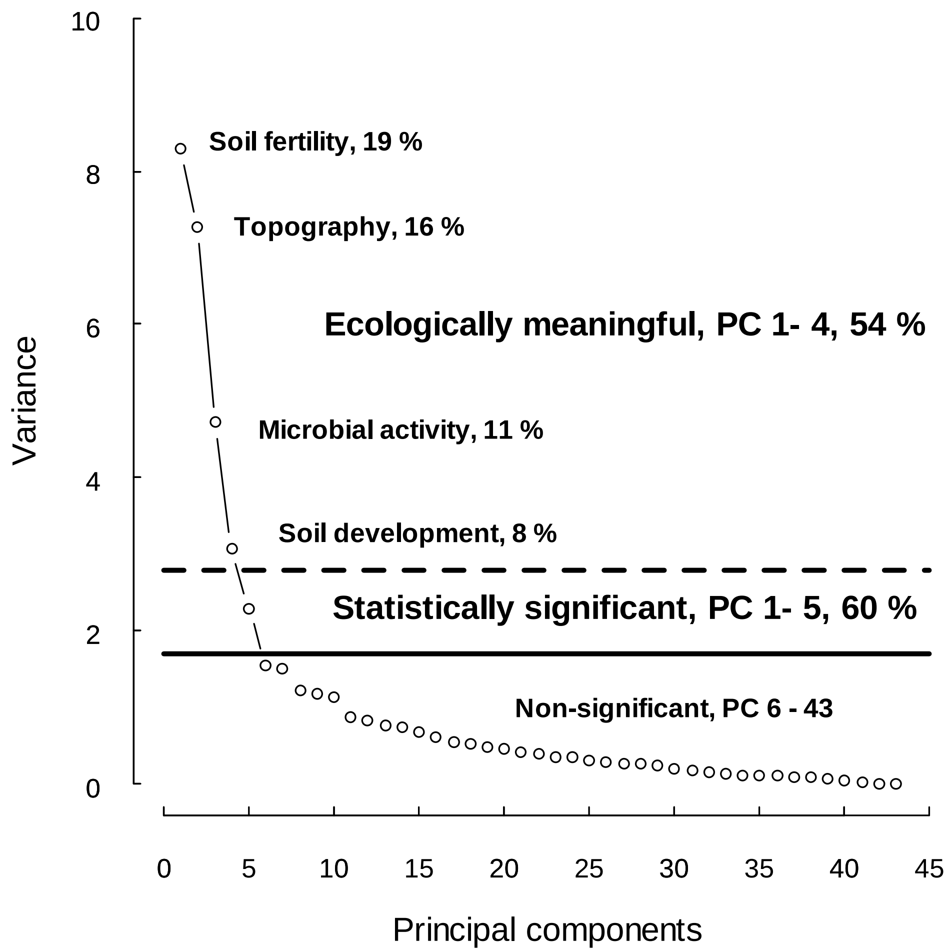

Figure 2.3. PCA scree plot. Ecologically meaningful, statistically significant and non-significant principal components and interpretation of the PCs with proportion of variance (%) explained. See text for explanation of interpretation.

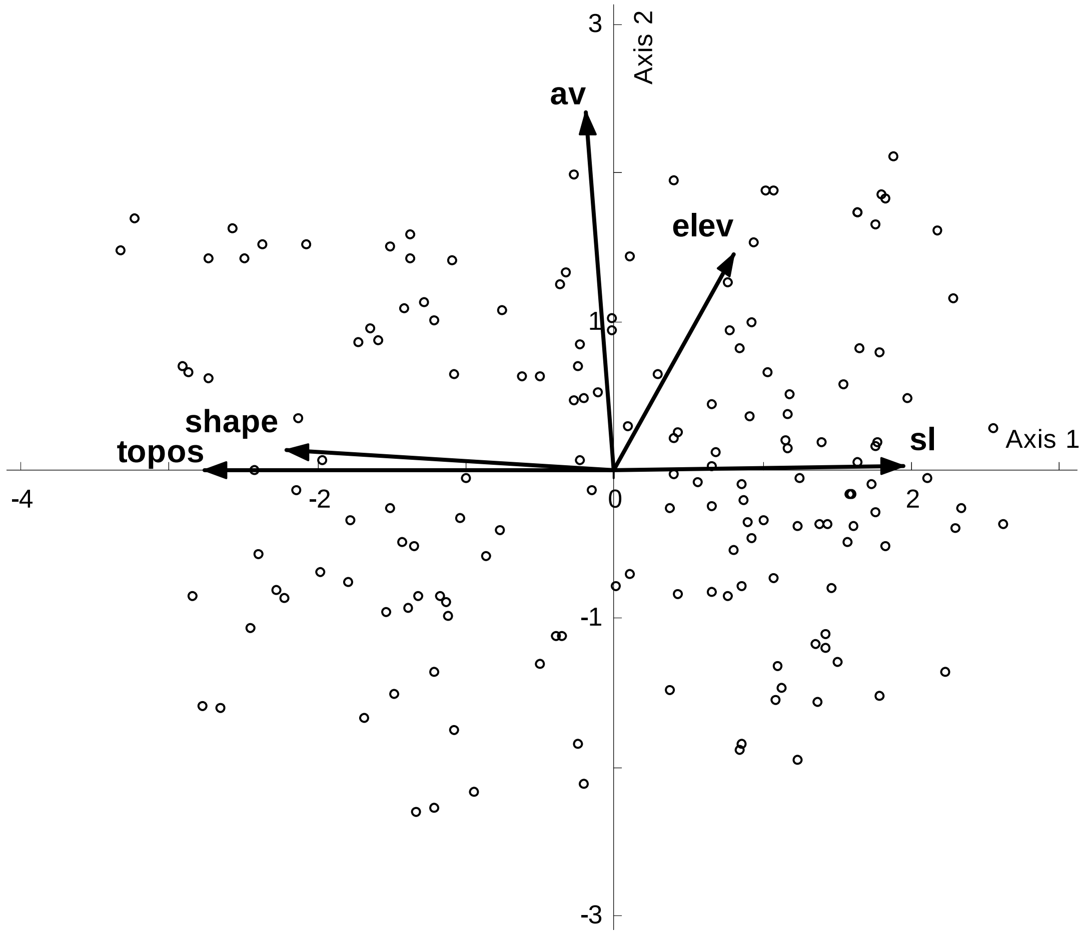

Figure 2.4. Joint plot of the second PCA run. Length (strength) and direction of the vectors show correlation of the physiographic variables in the ordination space. See text for explanation.

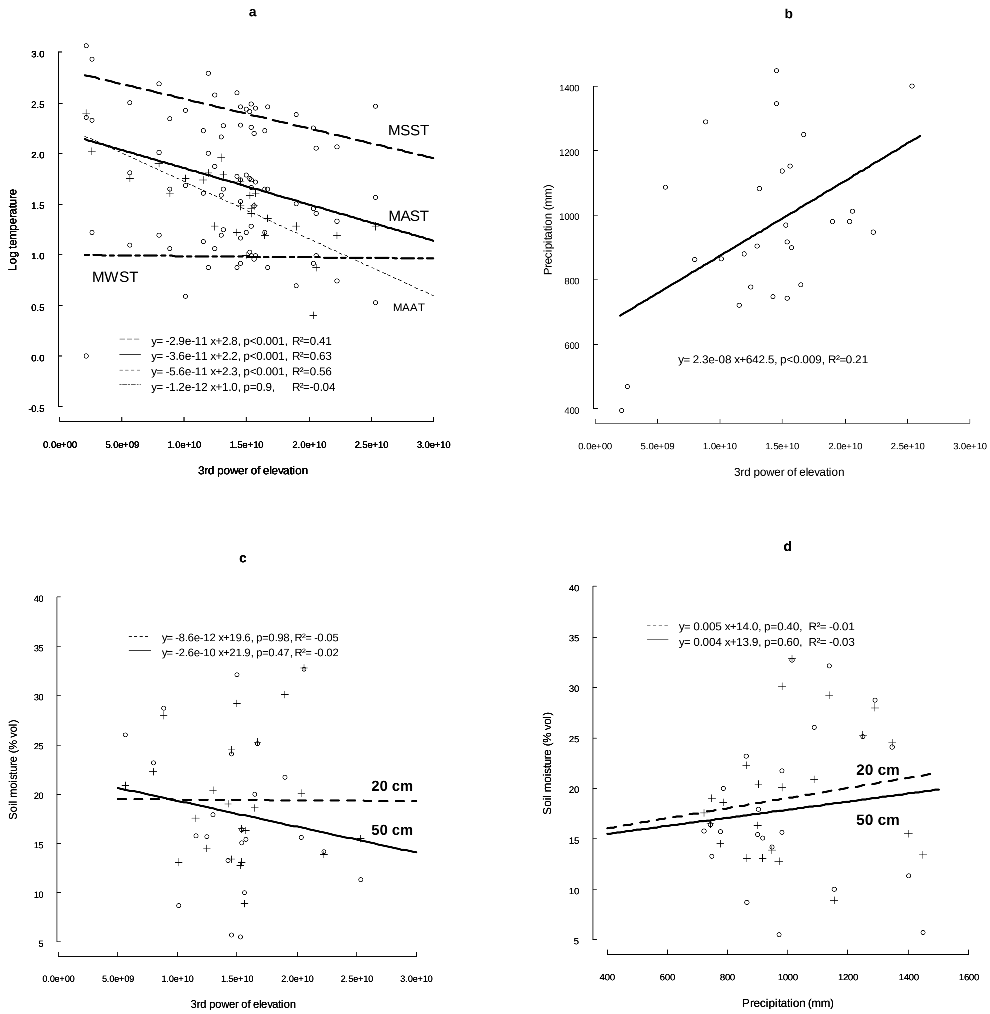

Figure 2.5. Relationship of: (a) air and soil temperatures, (b) precipitation, and (c) soil moisture with elevation; and (d) soil moisture with precipitation for the northern Wasatch Range, UT. Mean annual air temperature (MAAT), mean annual soil temperature (MAST), mean summer soil temperature (MSST), mean winter soil temperature (MWST). Soil moisture in 20 and 50 cm of soil depth.

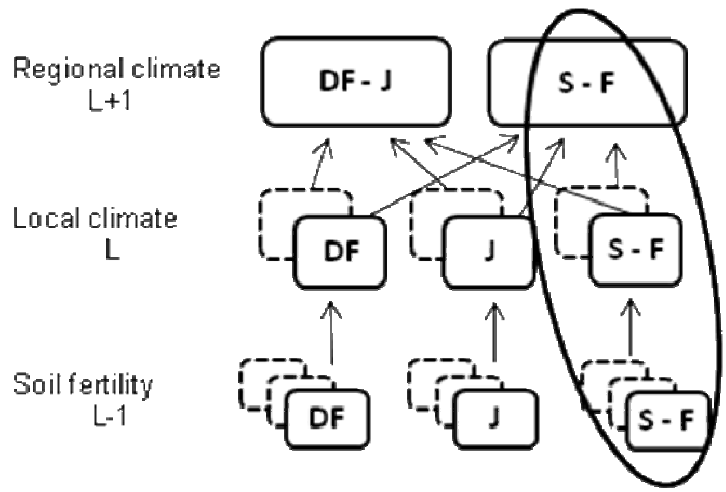

Figure 2.6. Hierarchical organization of forest ecosystems represented by spruce-fir (S-F), Douglas-fir-juniper (DF-J), Douglas-fir (DF), and juniper (J) communities. The oval represents the S-F zone in the earlier classifications. Arrows demonstrate agglomerative (bottom-up) approach; because of environmental compensation, e.g., S-F from the local climate (L) can be found either along valley bottoms inside the DF-J unit or on shaded slopes inside the S-F unit of the regional climate (L+1). The same S-F from the L level consists of either poor or rich S-F from the fertility level (L-1).

CHAPTER 3

VEGETATION GEO-CLIMATIC ZONATION IN THE ROCKY MOUNTAINS, NORTHERN UTAH [2]

Abstract

Fundamentals of the direct gradient analysis, hierarchical organization of terrestrial ecosystems together with approach of the biogeoclimatic classification used in British Columbia were used to develop a vegetation geo-climatic zonation in a mountainous study area in the northern Utah.

This classification was derived from sampling of forest (spruce-fir, Douglas-fir, aspen, juniper woodland) ecosystems on zonal sites, i.e., sites with mature vegetation, moderate topographic and intermediate soil characteristics. Thirty-five plots were described by vegetation, physiographic features and soil properties such as nutrient pools and dynamics. The SNOwpack TELemetry (SNOTEL) and The National Weather Service (NWS) Cooperative Observer Program (COOP) weather station network were used to approximate climate of sample plots.

Principal component analysis revealed the dominant role of regional climate in affecting broad vegetation pattern. We discriminated inside this pattern using cluster analysis, RandomForests classification and ANOVA and based on vegetation physiognomy, climatic data and taxonomic classification of zonal soils we identified two vegetation geo-climatic zones: (1) montane with Rocky Mountain juniper and Douglas-

[2] Coauthored by Antonin Kusbach, Helga Van Miegroet, James N. Long, and Janis L. Boettinger

fir; and (2) subalpine zone with Engelmann spruce and subalpine fir as climatic climax species.

This zonation will provide the framework for building a comprehensive ecosystem classification.

Introduction

"Without classification there is no science of ecosystems and ecology. And indeed, no science" - V. J. Krajina

Rocky Mountain ecosystems are complex in vegetation. A vegetation pattern i.e., species distribution, is affected by climate, topography, and geology as well as other abiotic and biotic factors such as disturbances and plant interactions. Environmental gradients are steep and the legacies of natural and anthropogenetic disturbances are pervasive (e.g., Gannet 1882, Barnes et al. 1982, McCune and Grace 2002, Shaw and Long 2007). Understanding these diverse ecosystems requires classification that accounts for the underlying complexity in important environmental drivers. Development of such a classification, in turn, requires a meaningful ecosystem organization using e.g., a triadic structure of the definitional levels in which the focal level "L" is between the next lower level "L-1", and the next higher level "L+1" (e.g., O'Neill et al. 1986, Urban et al. 1987, King 2005).

Such a hierarchical organization was created for the Rocky Mountains, northern Utah represented by the study area (Chapter 2). Regional climate as the highest level (L+1) was superimposed over local climate (the focal level, L) and soil fertility (the lowest level, L-1). We suggest the overarching influence of regional climate in this organizational hierarchy is strongly related to broad vegetation pattern or regional ecosystems (Klinka and Chourmouzis 1999, K. Klinka 2009, personal communication) such as e.g., life zones (Merriam 1890) or biogeoclimatic zones of mountains (Krajina 1965).

The level (L+1) in the ecosystem organization (regional climate) is suggestive of **the zonal (climatic climax) concept**. Originally formulated in terms of soil zonality (Dokuchaev around 1870), it expresses the relationship between climate, associated vegetation, and soils (e.g., White 1997). In other words, stable, i.e., late-seral or old growth (climatic climax) plant communities with intermediate edaphic conditions (relative to the extremes of a region) best reflect the influence of regional climate (Hills 1952, Krajina 1965, Pojar et al. 1987, Bailey 2002). Thus, local climatic, topographical and edaphic extremes such as those found on warm south-facing slopes, cool north-facing slopes, cold depressions or skeletal soils, are eliminated and only intermediate environmental conditions should be considered in the zonal concept application (Fig. 3.1).

Our overarching goal is to better understand broad vegetation patterns in a Rocky Mountain landscape. Specifically, we examine the relationships between vegetation and environmental variables for **zonal sites** (*sensu* Krajina 1965, Bailey 2002), sites with mature vegetation, moderate topographic and intermediate soil characteristics (i.e., intermediate site conditions) (Pojar et al. 1987, Klinka and Chormousis 1999). Our objective is to assess and classify the response of the complex vegetation to those environmental factors operating at the highest level of our ecosystem organization.

Methods

Study area

Franklin Basin (FB) is a montane-subalpine area, approximately 15,000 ha in size, situated between the Bear River Range and the Wasatch Range in the central Rocky Mountains on the Utah and Idaho border. The T.W. Daniel Experimental Forest (TWDEF), approximately 1,000 ha in size, is situated on the high ridge plateau of the Wasatch Range (10 km to the southeast of FB). Logan Canyon is lower in elevation and its upper part together with FB and TWDEF makes up the study area (ca 20,000 ha, and ca 1,400 m of vertical extent) (Fig. 2.2).

According to Bailey (1998) and McNab et al. (2007), the study area occurs within M331 Southern Rocky Mountains Steppe-Open Woodland-Coniferous Forest-Alpine Meadow Province, “D” Overthrust Mountain Section, “n” Northern Wasatch Range, and “o” Bear River Front Range Subsections. The mean annual precipitation ranges from about 720 to 1250 mm and mean annual air temperature ranges from 2.4 to 5.7 ^{o}C for Temple Fork, Tony Grove Lake, Franklin Basin, and Utah State University (USU) Doc Daniel weather stations (http://www.wcc.nrcs.usda.gov/snow/).

The terrain is mountainous, rocky and steep with occasional flat to gently sloping high ridge-plateaus and benches. The elevation ranges from 1590 to 3060 m across the three study sites. The highest area of the Bear River Range was glaciated during the Pleistocene as manifested by glacial geomorphologic features like moraines, U-shaped valleys, erratics, and irregular glacial deposits (Young 1939, Degraff 1976). The study area is mostly built from calcareous sedimentary rocks (limestone, dolomite) with interlayered quartzite, and from Tertiary sediments (grit, conglomerate, and siltstone of

Wasatch Formation) at the TWDEF site. The soils are formed in residuum, colluvium, alluvium, glacial till and outwash, and occur on diverse landforms such as cliffs, moraines, karst valleys, slopes, landslides, plains, valleys, depressions, ravines, and wetlands (Schoeneberger et al. 2002).

Over half of the study area is occupied by forest ecosystems including Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), woodland ecosystems including mountain mahogany (*Cercocarpus ledifolius*) and Rocky Mountain juniper (*Juniperus scopulorum*), and riparian, mostly willow (*Salix spp.*) ecosystems. Substantial changes in fire regimes, often in combination with cutting and grazing, have led to dramatic changes in the structure and the age-class distribution of forest stands. In many places, 100- to 140-year-old stands are now predominant (Long 1994). Forests in the study area are thus characterized by mid- and late-seral stages where forest understory is usually well developed (Pfister and Arno 1980).

Data collection

Ecosystems and their components change along an altitudinal gradient (e.g., Gannett 1882, Daubenmire 1943a, b, Whittaker and Niering 1965, Peet 2000, Shaw and Long 2007). We established 35 sample plots in the summers of 2006 and 2007 along a broad elevation range in order to capture broad climatic variation e.g., in temperature and precipitation. It was a part of a larger sampling design, but for this analysis we selected zonal sites i.e., mature forest stands with intermediate site characteristics such as mid-slope position, gentle to moderate slope (< 30 %), loamy soils > 50 cm deep with coarse rock fragment content < 50 % by volume and no growing-season water table (Pojar et al., 1987) (Fig. 3.1). In other words, slope position, gradient, aspect and shape do not strongly modify overall climate as in e.g., frost pockets, cold air drainages and on steep south/north-facing slopes. As “mature” we considered vegetation with relatively stable stand composition in which potential climax tree species are recognizable, and where a clear successional trajectory is discernible e.g., from advance regeneration of climax species (Pfister and Arno 1980, Pojar et al. 1987).

A stratified (based on vegetation physiognomy) fixed (subjective selection) sampling design was used with circular zonal plots size of 1000 m^2 (Brohman and Bryant 2005). We described each sample plot by species abundances (cover percentage) and by environmental variables such as relatively static or constant attributes i.e., physiographic variables (elevation, slope aspect, slope gradient, topographic position and slope shape (Lotspeich 1980); dynamic attributes such as O and A horizon thickness, humus form, pH, nutrient pools, attributes describing relatively slow processes; and attributes such as nutrient supply rates describing relatively fast processes (Table 2.1). Parent material observed on the sites was checked by geologic map (Dover 1995). One soil pit was dug in each plot to the unweathered parent material and described using the National Cooperative Soil Survey protocols (Soil Survey Staff 1999, 2006, Schoeneberger et al. 2002). Humus form was identified following Green et al. (1993).

A detailed description of the various site characterization methods was provided in Chapter 2. Briefly, one composite soil sample from 0-30 cm was collected from a pedon face in each plot, air dried and sieved (< 2 mm), and the fine fraction analyzed for texture classes (sandy, loamy, clayey) using the feel-method (Thien 1979). Samples were then analyzed for pH (1:1 soil in water, Corning pH analyzer) and total C and N (LECO CN analyzer, Leco Corp., St. Joseph, MI). Exchangeable cations using a mechanical vacuum extractor (Holmgren et al. 1977), followed by extractant analysis on inductively-coupled plasma spectrophotometer (ICP) (Iris Advantage, Thermo Electron, Madison, WI); extractable P [the Olsen P method (Olsen et al. 1954), sodium bicarbonate extraction, Thermo Electron Spectronic 20 Genesys spectrophotometer]; and mineralizable N [7-day anaerobic incubation and extraction (Keeney and Bremmer 1966), NH_4 analysis (Lachat Quickchem 8000 Flow Injection Analyzer)] were determined as a static-absolute nutrient availability index (SNAI).

To determine a dynamic-relative nutrient availability index (DNAI) (Qian and Schoenau 2002), plant root simulators (PRS™-probes; Western Ag Innovations, Inc., Saskatoon, Canada), a combination of anion and cation exchange membranes, were buried vertically into the mineral soil at each site for six weeks (during September and November). PRS™-probes were cleaned and sent to Western Ag Innovations for extraction and chemical analysis including Ca, Mg, K, S, Fe, Mn, Zn, Cu, Pb, Al, NH_4 cations, and NO_3 and PO_4 anions (Table 2.1).

Climatic data such as air temperature, precipitation, soil temperature, and soil moisture for the northern Wasatch Range [corresponding with M331D Section in McNab et al. (2007)] were obtained from nearby weather stations to approximate ambient and soil climate of the zonal sites. Soil temperature (50 cm depth) and moisture (20 cm and 50 cm depth) were measured daily on an open area, i.e., no tree canopy (R. Julander 2009, personal communication). Both the Natural Resources Conservation Service (NRCS) SNOwpack TELemetry (SNOTEL; http://www.wcc.nrcs.usda.gov/snow/) and the National Weather Service Cooperative Observer Program (COOP; http://www.nws.noaa.gov/om/coop/) station networks provide long term observations for air temperatures and precipitation (>10 years). Soil temperature and moisture at SNOTEL sites were available for six years (2003-2008, USU Doc Daniel for 2008-2009) and there were two COOP stations with soil temperature measurements for the northern Wasatch Range (Utah Climate Center; http://climate.usurf.usu.edu/). Accuracy of the analysis may therefore be limited by the short data record. Also no soil property information is available for the monitoring sites such as organic horizon, texture, and coarse rock fragment content. Nevertheless, these data were an important source of information in this analysis (Table 3.1).

Concepts of vegetation zones

Zones in earlier classifications i.e., life zones (Merriam 1890) or vegetation zones (Daubenmire 1943a, Peet 2000 based on Whittaker and Niering 1965) were named based on general physiognomy, i.e., dominant tree species (Whittaker 1972, Long 1994). For example, within the elevation range of the study area (1500 - 3000 m) there are juniper, Douglas-fir and Engelmann spruce-subalpine fir zones. Within those broad vegetation zones, environmental variation is large.

Aspen-dominated communities cover extensive areas in the Western U.S. (e.g., Rogers et al. 2010) and aspen is considered an extremely important component of many Rocky Mountain landscapes. There is continuous discussion about character of aspen in the Western U.S.; aspen is considered a pioneer, shade-intolerant species that may create either stable (persistent, climax) and unstable (seral) stands (e.g., Mueggler 1985, Kay

1997, Kulakowski et al. 2004, Shepperd et al. 2006, Kashian et al. 2007, Rogers et al. 2010) or even old-growth ancient forests (Peterson et al. 1995). Successional status of aspen communities, especially stable aspen, as well as the environmental conditions within the community is still ill-defined (Mueggler 1988). Typically, because of its successional status (pioneer tree species), aspen is not included within earlier vegetation zonations and has been classified separately (Mueggler 1988). To better understand the role of aspen in these landscapes and its response to environmental factors which might be influencing the distribution of conifer-dominated communities, aspen was included in this analysis despite to its pioneer and because of its putative stable/climax character. We sampled both mature conifer sites (< 15 % of aspen canopy cover) and aspen-dominated sites (> 85 % canopy cover, little or no conifer regeneration) (e.g., Mueggler 1985, Rogers et al. 2010).

Data analysis

In this data analysis, we performed the following analytical steps in order to reveal broad vegetation-site relationships: (1) grouping of vegetation data; (2) ordination of environmental data; (3) cluster analysis on the important environmental variables; (4) discriminant analysis by RandomForests of clusters base on important environmental variables; (5) ANOVA of vegetation groups; and (6) classification of zonal soils based on climatic data. The dataset was comprised of 35 zonal sites, 41 environmental variables and 18 tree and shrub species.

Vegetation grouping was performed as unsupervised cluster analysis of species abundances represented by cover percentage [flexible beta with β = -0.25, Sorensen distance (Bray and Curtis 1957)]. Identification of the vegetation groups was based on species constancy/frequency and dominance (e.g., Brohman and Bryant 2005, Winthers et al. 2005, Jennings et al. 2008). Species covers were subjected to square root transformation to approximate a normal distribution.

We used Principal components analysis (PCA) ordination (Pearson 1901) to determine the relative importance of the environmental variables and interpret principal components (PC) associated with zonal sites. Orthogonal rotations and correlation type of a cross-products matrix were used to get independent, mutually uncorrelated PCs (Lattin et al. 2003). Significance of PCs was tested by a Monte Carlo randomization test (based on proportion-based *p*-values for each PC). In order to document the relationship of the variables with the PCs and interpret PCs, we calculated correlation coefficients (loadings) with each ordination axis, and the linear (parametric Pearson's *r*) and rank (nonparametric Kendall's *tau*) relationships between the ordination scores and the observed variables. Our use of *r* and *tau* is suggested to be, even in relatively small datasets, more conservative than *p*-values for the null hypothesis of no relationship between ordination scores and variables (McCune and Grace 2002). We set the threshold for *r* and *tau* > 0.35. For variables conversion and transformation see Chapter 2.

To associate the vegetation groups with important environmental factors obtained in the PCA and to distinguish among them, we ran cluster analysis. Ward's linkage method with compatible Euclidian distance matrix has been often used as effective method of multivariate ecological data clustering (Ward 1963, McCune and Grace 2002). However, the best results were accomplished with Sorensen distance (Bray-Curtis coefficient) as suggested by McCune and Grace (2002). We transformed the variables with

|skewness|>1 to be close to multivariate normality and standardized the data by adjustment to standard deviate (*z*-scores). We checked the dataset for outliers given cutoff of 2.0 standard deviations from the grand mean (McCune and Mefford 2006). A clustering dendrogram was scaled by a distance objective function (Wishart 1969) and resulting height was used to decide how many clusters to retain (McCune and Grace 2002). The solution was verified by pseudo F function (Calinski and Harabasz 1974).

RandomForests analysis (Breiman 2001) was used to identify the most important environmental variables associated with meaningful zonal site clustering to highlight cluster differences. This machine-learning method is advantageous for classification of ecological data; it is accurate, combines many classification trees, and determines variable importance (e.g., Chen et al. 2004, Cutler et al. 2007).

Using the most important factors obtained from RandomForests classification and PCA, we assessed differences between the vegetation groups by 1-way ANOVA using Student-Newman-Keuls and Tukey's multiple comparison tests. The variables were transformed for normality by power or logarithmic transformation when necessary.

We used the climatic data (Table 3.1) such as air and soil temperature, precipitation, and soil moisture (obtained from SNOTEL and COOP weather stations) as approximation of ambient and soil climate of the zonal sites to classify soils following the National Cooperative Soil Survey (Soil Survey Staff 1999, 2006, Schoeneberger et al 2002). Based on daily soil temperature measurements at a depth of 50 cm from the soil surface, we calculated mean annual soil temperature (MAST), mean summer soil temperature (MSST) (June, July, and August in the Northern Hemisphere), and mean winter soil temperature (MWST) (December, January, February in the Northern

Hemisphere) (Soil Survey Staff 2006). We used daily soil moisture measurements at a depth of 20 and 50 cm (consistent with conditions for the soil moisture control section extent) for calculation of the mean soil moisture, mean number of dry consecutive days in the 4 months following the summer solstice, and mean number of moist consecutive days in the 4 months following the winter solstice (Soil Survey Staff 2006). We considered volumetric soil moisture content of 12 % as a general threshold between a dry and moist soil moisture control section for loamy soils (Brady and Weil 1999).

JUICE software ver. 7. 0. 41. (Tichý 2002), R software, ver. 2. 7. 2. (http://www.r-project.org/), SAS 9.1.3 Service Pack 4 software (http://www.sas.com/software/sas9/), and PC-ORD 5 (McCune and Mefford 2006) were used in the analysis.

Results

Vegetation grouping

Cluster analysis of species abundances resulted in the identification of five major vegetation groups based on both the most constant and dominant species. These groups are: Engelmann spruce, subalpine fir, Douglas-fir, Rocky Mountain juniper and aspen (Table 3.2).

Environmental ordination

We used the environmental data (Table 2.1) to run two PCAs: the first included all 35 sites (i.e., both conifer- and aspen-dominated sites); the second included only the 18 conifer-dominated sites. The most important principal component (PC1) in both PCA runs was associated with elevation, and soil properties such as A horizon thickness, humus form, rock fragment content, parent material, soil color, pH and nutrients (Table

3.3, 3.4). PC1 was interpreted as a **climate/geomorphology** gradient for both PCA cases, driven by elevation as the surrogate for regional climate (Chapter 2) and by geomorphology, which is reflected by parent material and soil properties (e.g., rock fragment content, color, pH and nutrients) (Fig. 3.2). Climate/geomorphology gradient explained 24 % of total variance in the entire dataset (with aspen) but explanatory power increased to 31 % in the reduced dataset (conifers), suggesting that inclusion of aspen-dominated sites in the analysis masked the importance of this major gradient. When the aspen-dominated sites were excluded, there was a dramatic increase in elevation loadings (Table 3.4). Therefore, the reduced conifer dataset results and twenty-three important environmental variables indicated by significant loadings in PC1 were used further to characterize the climate/geomorphology gradient.

The second principal component (PC2) in the reduced dataset (conifer) was associated with aspect value, organic horizon thickness, soil texture, and nutrients such as N, Ca, Mg, K, Al and P (Table 3.4). We interpreted this PC as indicative of **microbial activity** (Fig. 3.2). This activity influenced soil organic matter decomposition rate influencing organic horizon thickness as well as the nutrient/chemical environment. Warm south-facing slopes experienced enhanced nitrification as indicated by high nitrate DNAIs (Table 3.4). Interpretation of the PC2 and also PC3, which is not relevant to this chapter, is consistent with Chapter 2.

Cluster analysis

Twenty-three environmental variables with significant loadings in PC1 were used in cluster analysis to identify environmentally similar sites and their associations to internally homogeneous and mutually different clusters. In both the entire dataset and conifer analysis there were clearly a two-cluster solution based on the distance objective function and information retained (stability of the two-cluster solution was indicated by the longest horizontal distances of clusters' branches) (Fig. 3.3a, b), and confirmed by calculation of the Pseudo F function (Calinski and Harabasz 1974) with the highest pF value for the two-cluster solution. In the conifer clustering, this solution cleanly discriminated spruce-fir and juniper-Douglas-fir vegetation groups (Fig. 3.3b). In the entire dataset including aspen-dominated sites, clustering did not discriminate these aspen sites (Fig. 3.3a).

Discriminant analysis

The clustering revealed two important, approximately balanced (similar number of observation) clusters/classes (Breiman and Cutler 2005, Chen et al. 2004) that were internally homogeneous and mutually different. RandomForests classification identified those environmental variables most strongly associated with this two-cluster solution. The clusters/classes represented different environments based on twenty-three important environmental variables. As a RandomForests result, there was a distinct break in the ranked variables discriminating more important from less important variables. Four environmental variables were identified as the most important factors discriminating the clustering of sites. In order of apparent importance, they were: Ca, K, elevation and Mn (Fig. 3.4). Except for elevation, all referred to soil nutrient status. “Out-of-bag” estimate of error rate as a measure of RandomForests misclassification was 6 %.

ANOVA

1-way ANOVA revealed overall significant differences between the vegetation groups represented by the conifer-dominated sites in the important variables identified by RandomForests using F-test and verified by p values (Ca SNAI: $F = 4.57$, $p = 0.0053$; K SNAI: $F = 7.02$, $p = 0.0006$; elevation: $F = 15.32$, $p < 0.0001$; Mn DNAI: $F = 6.53$, $p = 0.0007$). Based on Student-Newman-Keuls and Tukey's multiple comparison tests, the juniper and Douglas-fir groups were not significantly different in terms of the important variables; neither were the subalpine fir and Engelmann spruce groups. The aspen group was not significantly different from the spruce and fir group, but was different from the juniper and Douglas-fir group (no aspen-dominated sites sampled in the lowest elevations) (Fig. 3.5, Table 3.5).

Therefore, we combined the four conifer-dominated groups into two final physiognomic groups: the composite juniper/Douglas-fir group we referred to as **montane**; and the composite Engelmann spruce/subalpine fir group we referred to as **subalpine**. The two resulting physiognomic groups differed from each other in all important environmental variables (Ca SNAI: $F = 7.39$, $p = 0.0023$; K SNAI: $F = 9.99$, $p = 0.0005$; elevation: $F = 24.50$, $p < 0.0001$; Mn DNAI: $F = 9.19$, $p = 0.0007$). Student-Newman-Keuls and Tukey's pairwise tests showed that the four important variables behaved consistently across the physiognomic groups; these are significantly different.

Based on clustering, classification and ANOVA the subalpine and montane physiognomic groups differed from each other based on climate/geomorphology. Aspen-dominated sites did not differ from the subalpine physiognomic group but differed from the montane physiognomic group (Fig. 3.5, Table 3.5).

Microbial activity (PC2) was associated with pronounced nitrification on gentle warm (i.e., south-facing) slopes. We focused on significant indicators of N availability i.e., mineralizable nitrogen and nitrate DNAI (Table 3.4). Once again, the vegetation groups were associated with distinctly different microbial activity (PC2) based on slope aspect, nitrogen DNAIs; (slope aspect: $F = 9.26$, $p = 0.0002$; Nmin DNAI: $F = 12.61$, $p < 0.0001$; NO_3 DNAI: $F = 14.36$, $p < 0.0001$). Student-Newman-Keuls pairwise test showed significant difference between the Douglas-fir and juniper group in slope aspect, mineralizable nitrogen and nitrate DNAI ($\alpha = 0.05$). Tukey's pairwise test showed significant difference between the Douglas-fir and juniper groups in nitrate DNAI (Table 3.5). These results implied that different aspects even on mild slopes may contribute to differences in nitrification resulting differences in the Douglas-fir and juniper group occurrence.

Classification of zonal soils

In the mountains of northern Utah, elevation is a good predictor of air temperature, soil temperature and also precipitation (Chapter 2). Despite the significant change of mean soil temperature with elevation, (except mean winter soil temperature - MWST due to snowpack insulation, Van Miegroet et al. 2000), regression results of the SNOTEL and COOP climatic data (Chapter 2) cannot be used to estimate temperature regime of zonal soils because of: (1) absence of climate station data from lower elevation forested soils; and (2) absence of tree cover type and O horizon information at the monitoring sites. Tree cover may have an influence on soil temperature regime as it transformes air temperature fundamentally. We estimated soil temperature regime based on Munk's (1988) measurements of soil temperatures under different tree canopy types in Logan Canyon, northern Utah. The soil temperature regime of soils under spruce-fir and aspen was classified as **cryic**, and under Douglas-fir and Rocky Mountain juniper as **frigid** (Soil Survey Staff 2006).

Soil moisture was not significantly related to either elevation or precipitation (Chapter 2); soil physical properties such as texture, depth, and coarse fragment content may be superimposed over the effect of overall climate represented by elevation. Because these soil physical properties were not available for the climate stations and calculation of the number of dry and moist consecutive days was inconclusive (Table 3.1), we used earlier measurements of soil moistures under different tree canopy types again supported by the data of nearby weather stations to estimate soil moisture regime. The soil moisture regime of soils under spruce-fir and aspen was classified as **udic**, and under Douglas-fir and Rocky Mountain juniper as **xeric** (Munk 1988, Soil Survey Staff 2006).

Soils in the montane group (juniper and Douglas-fir communities) were classified as Pachic and Typic Argixerolls in the soil order of **Mollisols**. The majority of soils in the subalpine group (subalpine fir and Engelmann spruce communities) were classified as Typic and Eutric Haplocryalfs in the soil order of **Alfisols** (Appendix A) (Soil Survey Staff 2006). Soil classifications of both physiognomic groups was consistent with e.g., Burns and Honkala (1990) and Erikson and Mortensen (1974). The majority of soils under aspen community were classified as Pachic and Typic Palecryolls, Typic Argicryolls, and Typic Haplocryolls (**Mollisols)** (Appendix A, Table 3.6). As in the montane zone, Mollisols indicate thick A horizon, soil organic matter accumulation and huge potential for C storage.

The parent material of subalpine zonal soils was mostly Pleistocene glacial deposits (moraine till) and Eocene sediments (grit, conglomerate, siltstone). Montane zonal soils have been formed in late Pleistocene - Holocene fluvio-colluvial deposits derived from Ordovician and Cambrian calcareous sediments.

Significant difference between the physiognomic groups in elevation (Fig. 3.5) together with strong relationships between elevation and climate suggested important climatic difference between these groups. This climatic difference combined with differences in geomorphology contributes to substantial soil differences among the physiognomic groups and distinguishes zonal soils at the level of soil order (Table 3.6).

Discussion

Our analysis, based on a broad range of data (vegetation, climate, and geomorphology) revealed a strong altitudinal pattern within the highest level (L+1) of our hierarchical ecosystem organization. At this level of organization, we distinguished two firm vegetation geo-climatic zones: the montane or lower mountain and the subalpine or upper mountain zone. These zones occur as stacked broad vertical belts with dramatic climatic, vegetation and geomorphologic differences.

The montane zone is characterized by Rocky Mountain juniper and Douglas-fir as the potential climatic climax species. The zone is warmer and drier than the subalpine zone; these climatic properties together with different parent material and rich understory vegetation are reflected by fertile Mollisols, which are also younger than the subalpine zonal soils. Higher potential productivity of the montane Mollisols is indicated not just by thick A horizons, but also by significantly higher concentrations of important macronutrients Ca and K contributing to higher soil alkalinity (Table 3.6). Because there was no significant difference between Douglas-fir and juniper communities in important environmental factors, and because there were relatively few zonal Douglas-fir-dominated stands (> ca 1000 m^2), we did not separate a Douglas-fir vegetation geo-climatic zone in the northern Wasatch Range.

Rocky Mountain juniper and Douglas-fir can form mixed-species stands on zonal sites. Floristic differences between Douglas-fir and juniper-dominated sites within the montane zone may result from: (1) different shade tolerance of these two species; and potentially (2) differences in N availability and form (either ammonium mineralization or nitrification). For example, increased insolation on south-facing slopes may limit Douglas-fir reproduction via failed seed germination or low seedling survival (Bates 1923, Burns and Honkala 1990). The shade-tolerance and requirement of a species may be increased on warm dry sites (Krajina 1965, 1969, Klinka and Chormousis 1999). Whereas Douglas-fir is intermediate in shade-tolerance compared to many of its associates (Burns and Honkala 1990), it may require more shade protection for establishment in semiarid conditions (Krajina 1965, 1969). Juniper, on the other hand, is a very shade-intolerant species (i.e., requires light exposure particularly light from above) in the later life stages (e.g., Burns and Honkala 1990). If Douglas-fir is able to establish, it has the potential to overtop and outcompete juniper (e.g., in thicker secondary growth).

Generally, conifers such as spruces (*Picea*), firs (*Abies*) and pines (*Pinus*) are physiologically adapted to high ammonium levels in soils; they take up ammonium preferentially (Yanai et al. 2009, Hangs et al. 2003, Bedell et al. 1999, Olsthoorn et al. 1991). Similarly, for Douglas-fir in dry conditions of south-facing slopes, uptake of ammonium is limited by its relative immobility (Gijsman 1991), but it is still preferred to nitrate (Kamminga-van Wijk and Prins 1993). Junipers appear to prefer nitrate to ammonium (Miller et al. 1991, Stark and Hart 1997) and may therefore be more competitive in high nitrification environments. Also allelopathic properties of Rocky Mountain juniper can inhibit establishment of other plants including Douglas-fir (e.g., Peterson 1972, Horman and Anderson 2003). Our ANOVA PC2 results are consistent with pronounced nitrification, and possibly low availability of ammonium, restricting Douglas-fir regeneration on south-facing slopes.

Engelmann spruce and subalpine fir are the climatic climax species for **the subalpine zone** at higher elevation. The zone is cooler and moister than the montane zone. A major portion of the zone in the study area has a glacial history (Young 1939, Degraff 1976) and soils have experienced frequent climatic changes during the Pleistocene (Buol et al. 2003). Lower productivity and higher acidity of the subalpine Alfisols is indicated by significantly lower Ca and K concentrations and higher Mn supply rate (Table 3.6). The higher amount of this metal is associated with more humid subalpine conditions likely facilitating release of this metal from parent material.

Engelmann spruce and subalpine fir are both very shade-tolerant tree species. They are commonly found in mixtures with spruce dominance in old growth and late-seral stands (e.g., Aplet et al. 1988, Peet 2000). In lower, more accessible parts of the subalpine zone within the study area, subalpine fir tends to be more abundant than spruce, probably the result of pioneer logging which favored removal of spruce. As a result of the logging history, we suspect Engelmann spruce is still somewhat underrepresented in second growth mid-seral stands.

The ecological amplitude of aspen is extremely broad in comparison with the conifers. This amplitude is climatic, as represented by aspen's large elevation range, and geomorphologic, as indicated by its occurrence on diverse soil parent materials (Fig. 3.5, Table 3.6). The wide range of climate and geomorphology is associated with large differences in nutrient availability among soils in aspen-dominated sites. Aspen occurs on rich sites with surpluses of macronutrients such as N, K, Ca, Mg. It also occurs on relatively poor sites where some secondary macronutrients may be deficient (Ca, Mg) and micronutrients such as Mn are in surplus. There is no single environmental factor, important at the level of regional climate, that can discriminate aspen as a discrete vegetation geo-climatic zone; this confirms the exceptionally broad ecological amplitude (e.g., Mueggler 1988, Klinka et al. 1999) and it is consistent with high genetic variability of trembling aspen (Mock et al. 2008).

There is no alpine vegetation geo-climatic zone in the study area and probably in the northern Wasatch Range because of the absence of alpine zonal sites in the highest elevations (over 3000 m). The northern Wasatch Range is not high enough for the alpine zone.

True zonal sites are rare in the central Rocky Mountains, Utah because of: (1) a rough, mountainous landscape (Barnes et al. 1982) and "accidents of topography" (Gannet 1882), meaning that "abruptness of elevation change over the local landscape can appear more important than absolute elevation" (Shaw and Long 2007); and (2) many ecosystems never reach potential climax due to natural disturbances such as fire (e.g., Pojar et al. 1987, Cook 1996) and human-caused disturbances such as past logging. Since zonal sites are scarce, a compromise was necessary in site selection during this study.

Rather than restricting sampling exclusively to old-growth, we included sites with mature, mid- to late-seral stands with well developed understory reflecting an obvious successional trajectory (Pfister and Arno 1980, Pojar et al. 1987).

Our vegetation geo-climatic zonation is explicitly framed by the highest definitional level (L+1), i.e., regional climate and geomorphology, in a hierarchical ecosystem organization. There is general consistency in our approach with the earlier vegetation zonation of Merriam (1890) based on an idea of broad life zones depending on overall climate (Chapter 2). However, there is a substantial difference between our approach and the vegetation zonation of Daubenmire (1943a), in that his approach is entirely based on vegetation without specific environmental information.

There may be a compensating influence of environmental factors on plants, and because of that compensation the same climax vegetation may appear over a broad environmental range (Pojar et al. 1987). For example, Engelmann spruce-subalpine fir (S-F) communities occur in the high-elevation subalpine vegetation geo-climatic zone; however they may also descend into the lower montane vegetation geo-climatic zone on shady slopes or as riparian/wetland communities along valley bottoms. In the subalpine zone, precipitation is higher, affecting S-F occurrence in intermediate conditions (on zonal sites). In the lower montane zone with lower precipitation, this decrease of water input may be compensated by supply and retention of water in locally specific conditions (local topography) such as shady slopes and valley bottoms. Local environmental conditions thus modify the influence of the low-elevation regional climate in the montane vegetation geo-climatic zone (Chapter 2). As a result, S-F communities can occur on lower elevation sites where there is enough moisture available.

Whereas Daubenmire (1943a) described spruce-fir, Douglas-fir, juniper and mountain mahogany communities as representatives of four different zones dependent on “ecologic criteria” represented by climate/elevation, we consider these communities to represent local topo-edaphic variations within a single vegetation geo-climatic zone. Such large environmental variations (accompanied by environmental compensation) are thus reflected by floristic differences within a vegetation geo-climatic zone. By specifying floristic differences between the vegetation geo-climatic zones, we can explain many special cases such as interfingering, telescoping, discontinuity and inversion of earlier vegetation zones (Daubenmire 1943a) that reflect the lower (local) level L (i.e., local topography and soil moisture, Chapter 2). It is apparent that the Daubenmire zonation combined the regional L+1 with the local L (topography-moisture) levels. Peet’s (2000) improved zonation by explicitly differentiating two factors, represented by elevation and topography-moisture, but keeping earlier vegetation zones *sensu* Daubenmire inside that framework.

There is great potential value of vegetation geo-climatic zonation; by keeping the L+1 level separate we contributed to “understanding of the discontinuity of the historical and environmentally broad vegetation zones” (Shaw and Long 2007). We argue that firm altitudinal belts exist in the central Rocky Mountains (Daubenmire 1943a). The vegetation geo-climatic zonation distinguished at the L+1 level will serve as the framework for further detailed ecosystem structuring at the lower levels.

There is consistency between Hierarchical Framework of Ecological Units (Cleland et al. 1997, ECOMAP 2007), the Terrestrial Ecological Unit Inventory (TEUI) Technical Guide (Winthers et al. 2005), and vegetation geo-climatic zonation; as regional climatic units the zones match sections, subsections and landtype associations units of subregions and landscapes in ECOMAP/TEUI standard (Table 2.4. in Chapter 2).

Summary and conclusions

Based on the zonal concept and the ecosystem organizational hierarchy, we defined two vegetation geo-climatic zones as areas with the same floristic structure in climatic climax. These zones were: **montane** with juniper/Douglas-fir; and **subalpine** with Engelmann spruce/subalpine fir as climatic climax species. We characterized these zones based on regional physical environment (i.e., climate and landform geomorphology/soils); with regional climate represented by elevation, precipitation and air and soil temperatures; and geomorphology by soil types. Aspen was excluded from the zonation due its great ecological amplitude. Even stable or climax aspen was not considered as zonal (climatic climax) vegetation. We suggest both the montane and subalpine zones match the subregion and landscape scale of the ECOMAP/TEUI classification.

The vegetation geo-climatic zonation outlined in this paper is a conceptual improvement on earlier approaches to vegetation zonation in the region. As a next step, the vegetation geo-climatic zonation can be used as a framework for additional structuring e.g., site classification, and in building a comprehensive ecosystem classification.

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Table 3.1. Climatic data for the northern Wasatch Range. SNOwpack TELemetry weather stations (SNOTEL), the National Weather Service Cooperative Observer Program weather stations (COOP), mean annual precipitation (MAP), mean annual air temperature (MAAT), mean annual soil temperature at 50 cm (MAST), mean summer soil temperature at 50 cm (MSST), mean winter soil temperature at 50 cm soil depth (MWST), mean soil moisture at 20 cm (Moist20), and 50 cm soil depth (Moist50), mean number of dry consecutive days at 20 cm (Dcon20), and 50 cm soil depth (Dcon50), mean number of moist consecutive days at 20 cm (Mcon20) and 50 cm soil depth (Mcon50). The stations in the study area and closest vicinity are in bold. NA-not applicable.

Station ID	Station	Elevation (m)	MAP (mm)	MAAT (C)	MAST (C)	MSST (C)	MWST (C)	Moist20 (% vol)	Moist50 (% vol)	Dcon20	Dcon50	Mcon20	Mcon50
COOP427 598	SLC INT AP	1286	394	11.00	10.60	21.50	0.00	NA	NA	NA	NA	NA	NA
COOP425 194	LOGAN EXP. FARM	1369	469	7.60	10.30	18.80	2.40	NA	NA	NA	NA	NA	NA
SNOTEL333	BEN LOMOND TR.	1776	1087	5.80	6.10	12.20	2.00	20.90	26.00	48	0	123	123
SNOTEL582	LITTLE BEAR	1995	862	6.70	7.50	14.70	2.30	22.30	23.20	5	0	123	123
SNOTEL1054	FARMINGTON L.	2066	1289	5.00	5.20	10.40	1.90	28.00	28.70	7	11	123	123
SNOTEL906	DRY FORK	2162	865	5.80	5.40	11.30	0.80	13.10	8.70	92	114	121	85
SNOTEL1013	**TEMPLE FORK**	**2257**	**721**	**5.70**	**5.00**	**9.30**	**2.10**	**17.60**	**15.80**	**30**	**98**	**109**	**88**
SNOTEL684	PARLEY'S SUM.	2286	879	6.10	7.40	16.40	1.40	NA	NA	NA	NA	NA	NA
SNOTEL763	SMITH & MOREH.	2316	777	3.60	6.50	13.20	1.90	14.50	15.70	50	97	123	106
SNOTEL1039	CASCADE MNT.	2348	903	7.10	4.90	8.70	2.30	20.40	17.90	78	87	122	109
SNOTEL971	PARRISH CREEK	2359	1082	6.00	5.20	9.70	2.50	NA	NA	NA	NA	NA	NA
SNOTEL374	BUG LAKE	2423	748	3.40	5.90	13.50	1.40	19.00	13.30	35	52	107	66

SNOTEL332	BEN LOMOND P.	2438	1448	5.60	5.70	11.70	2.20	13.40	5.70	79	121	122	4
SNOTEL474	FARMINGTON	2438	1347	4.40	4.60	9.80	1.50	24.50	24.10	51	90	122	122
SNOTEL484	**FRANKLIN BASIN**	**2464**	**1137**	**2.70**	**6.00**	**11.50**	**2.40**	**29.20**	**32.10**	**1**	**0**	**123**	**123**
SNOTEL820	TIMPANOGOS DIV.	2481	970	4.90	5.80	11.20	1.80	12.80	5.50	69	123	122	9
SNOTEL533	HORSE RIDGE	2487	917	4.30	5.70	12.10	1.70	13.10	15.10	103	90	123	115
SNOTEL393	CHALK CREEK #2	2487	742	4.10	5.30	9.60	2.60	16.50	16.40	58	101	107	107
SNOTEL596	LOOKOUT PEAK	2500	1153	4.40	4.40	9.00	1.60	8.90	10.00	97	90	45	95
SNOTEL1056	LIGHTNING RIDGE	2504	899	5.00	5.60	11.60	1.70	16.30	15.40	NA	NA	NA	NA
SNOTEL1098	**USU DOC DANIEL**	**2521**	**1055**	**2.40**	**NA**	**NA**	**NA**	**22.70**	**16.50**	**8**	**39**	**122**	**18**
SNOTEL455	DRY BREAD POND	2545	785	3.30	5.20	9.30	2.40	18.60	20.00	52	92	123	123
SNOTEL823	**TONY GR. LAKE**	**2556**	**1250**	**3.90**	**5.20**	**11.70**	**1.40**	**25.30**	**25.10**	**38**	**0**	**122**	**0**
SNOTEL366	BRIGHTON	2667	980	3.60	4.50	10.90	1.00	30.10	21.70	6	48	122	122
SNOTEL634	MONTE CRISTO	2731	981	1.50	4.30	9.50	1.50	20.10	15.60	53	73	123	105
SNOTEL392	CHALK CREEK #1	2741	1013	2.40	4.10	7.80	1.70	32.80	32.70	0	0	122	122
SNOTEL814	THAYNES CYN	2813	947	3.30	3.80	7.90	1.10	13.90	14.20	74	65	56	71
SNOTEL766	SNOWBIRD	2938	1400	3.60	4.80	11.80	0.70	15.50	11.30	62	83	109	15

Table 3.2. Vegetation analysis of tree communities. Bold tree species indicate both the most constant and dominant species and are indicators for the particular tree community. Constant species percentage means the proportion of the plots in which species occurs; all species with the threshold value ≥ 60 % are displayed. E.g., *Picea engelmannii* 100 means that this species occurs on 100 % of the sample plots within the vegetation group 1. Dominant species percentage means the proportion of the plots, in which species occurs with cover ≥ the threshold value for dominant species; all species with the threshold value ≥ 40 %; 20 % for thin juniper woodland are displayed. E.g., *Picea engelmannii* 50 means that this species occurs on 50 % of the sample plots with cover ≥ 40 % within the vegetation group 1.

Vegetation group 1
Number of plots: 8
Threshold value for constant species: 60
Threshold value for dominant species: 40

Constant species: ***Picea engelmannii* 100**, *Abies lasiocarpa* 100, *Populus tremuloides* 75
Dominant species: ***Picea engelmannii* 50**

Vegetation group 2
Number of plots: 3
Threshold value for constant species: 60
Threshold value for dominant species: 40

Constant species: ***Abies lasiocarpa* 100**, *Picea engelmannii* 100, *Populus tremuloides* 100, *Symphoricarpos oreophilus* 67, *Sambucus cerulea* 67, *Pseudotsuga menziesii* 67, *Amelanchier alnifolia* 67
Dominant species: ***Abies lasiocarpa* 33**

Vegetation group 3
Number of plots: 17
Threshold value for constant species: 60
Threshold value for dominant species: 40

Constant species: ***Populus tremuloides* 100**, *Symphoricarpos oreophilus* 94, *Abies lasiocarpa* 71
Dominant species: ***Populus tremuloides* 94**, *Symphoricarpos oreophilus* 6

Vegetation group 4
Number of plots: 4
Threshold value for constant species: 60
Threshold value for dominant species: 20
Constant species: ***Juniperus scopulorum* 100**, *Pseudotsuga menziesii* 100, *Symphoricarpos oreophilus* 75, *Prunus virginiana* 75
Dominant species: ***Juniperus scopulorum* 75**

Vegetation group 5
Number of plots: 3
Threshold value for constant species: 60
Threshold value for dominant species: 40

Constant species: ***Pseudotsuga menziesii* 100**, *Juniperus scopulorum* 100, *Amelanchies alnifolia* 100, *Symphoricarpos oreophilus* 100, *Prunus virginiana 67, Abies lasiocarpa 67*
Dominant species: ***Pseudotsuga menziesii* 100**

Table 3.3. PCA summary. Significant principal components are in bold.

Entire dataset (with aspen)	**PC1**	**PC2**	**PC3**	**PC4**	PC5	PC6	PC7	PC8	PC9	PC10
Eigenvalue	**10.03**	**6.49**	**4.43**	**3.85**	2.19	1.73	1.56	1.47	1.18	1.03
% of Variance	**24.46**	**15.82**	**10.80**	**9.39**	5.35	4.21	3.80	3.57	2.88	2.51
Cumulative % of Var.	**24.46**	**40.28**	**51.08**	**60.47**	65.81	70.03	73.82	77.39	80.27	82.78
p- value	**0.0002**	**0.0002**	**0.0002**	**0.0002**	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Conifer dataset										
Eigenvalue	**12.75**	**6.29**	**4.65**	3.65	2.69	2.12	1.74	1.29	1.22	1.16
% of Variance	**31.09**	**15.34**	**11.34**	8.90	6.65	5.17	4.24	3.14	2.98	2.83
Cumulative % of Var.	**31.09**	**46.43**	**57.77**	66.68	73.24	78.41	82.65	85.79	88.77	91.59
p- value	**0.0002**	**0.0002**	**0.0439**	0.7752	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000

Table 3.4. PCA loadings. Significant Pearson's (r), and Kendall's (*tau*) coefficients are in bold; both significant r and *tau* express a significant variable for the particular PC (shaded). Variables are defined in Table 2.1.

	Entire dataset				**Conifer dataset**			
Variable	**PC1**		**PC2**		**PC1**		**PC2**	
	r	**tau**	**r**	**tau**	**r**	**tau**	**r**	**tau**
elev	**-0.52**	**-0.37**	**-0.55**	-0.31	**-0.84**	**-0.54**	0.03	-0.09
topos	**0.43**	**0.38**	**0.39**	0.30	0.34	0.30	-0.24	-0.19
sl	0.12	0.13	-0.29	-0.15	0.25	0.25	**0.36**	0.29
av	**-0.49**	-0.31	**0.48**	0.28	**-0.36**	-0.13	**0.53**	**0.46**
shape	0.28	0.25	0.15	0.11	0.07	0.02	0.08	0.07
Ohor	**-0.67**	**-0.46**	**0.50**	0.32	**-0.48**	-0.19	**0.72**	**0.64**
Ahor	**0.76**	**0.60**	-0.21	-0.19	**0.62**	**0.40**	-0.15	-0.05
hum	**0.73**	**0.49**	**-0.43**	-0.20	**0.65**	**0.50**	**-0.50**	-0.30
sdepth	0.25	0.18	**0.50**	0.27	0.24	0.14	0.01	-0.06
RF	**-0.55**	**-0.40**	**-0.43**	-0.28	**-0.66**	**-0.56**	-0.19	-0.17
parmat	**0.68**	**0.54**	0.20	0.04	**0.56**	**0.45**	0.12	0.12
mottles	0.33	0.22	-0.04	-0.07	**0.60**	**0.49**	0.14	0.11
cvalue	**-0.73**	**-0.57**	-0.05	-0.02	**-0.67**	**-0.58**	-0.14	-0.02
text	0.18	0.12	**0.42**	**0.37**	**0.52**	**0.43**	**-0.56**	**-0.43**
pH	**0.56**	**0.37**	**0.42**	0.23	**0.69**	**0.48**	0.23	0.07
Nmin_d	0.31	0.24	**-0.84**	**-0.61**	-0.11	-0.11	**-0.66**	**-0.46**
Nox	**0.85**	**0.64**	-0.08	-0.10	**0.68**	**0.48**	0.30	0.22
NO3_d	**0.38**	0.30	**-0.82**	**-0.60**	0.08	0.04	**-0.61**	**-0.44**
NH4_d	**-0.43**	-0.34	0.07	0.09	**-0.64**	**-0.44**	-0.31	-0.19
Cox	**0.69**	**0.55**	-0.01	-0.13	**0.62**	**0.41**	**0.38**	0.24

C/N	**-0.62**	**-0.38**	0.15	0.12	**-0.62**	**-0.39**	-0.11	-0.03
Ca_d	**0.38**	0.26	**-0.35**	-0.26	0.13	0.15	**-0.72**	**-0.46**
Mg_d	**0.40**	0.32	-0.23	-0.16	0.07	0.02	**-0.74**	**-0.49**
K_d	-0.16	-0.10	-0.29	-0.24	-0.24	-0.16	**0.63**	**0.50**
P_d	0.25	0.19	-0.28	-0.24	0.03	-0.01	-0.16	-0.21
Fe_d	-0.01	0.01	**-0.76**	**-0.60**	**-0.57**	**-0.36**	-0.19	-0.08
Mn_d	**-0.60**	**-0.37**	**-0.62**	**-0.41**	**-0.89**	**-0.71**	-0.17	-0.20
Zn_d	0.34	0.22	**-0.69**	**-0.55**	-0.08	-0.16	-0.19	-0.14
S_d	-0.30	-0.19	**-0.52**	-0.33	**-0.67**	**-0.56**	-0.03	-0.10
Al_d	0.00	0.06	-0.22	-0.15	-0.15	-0.14	**-0.87**	**-0.80**
Ca_s	**0.82**	**0.59**	0.29	0.21	**0.95**	**0.79**	0.10	0.07
Mg_s	**0.73**	**0.59**	0.32	0.23	**0.77**	**0.58**	-0.33	-0.16
K_s	**0.35**	0.26	**0.41**	0.26	**0.89**	**0.67**	0.20	0.14
NH4_s	0.21	0.18	**-0.45**	-0.34	**-0.36**	-0.28	0.16	0.05
Nmin_s	**0.72**	**0.60**	-0.15	-0.12	**0.73**	**0.62**	0.21	0.22
P_s	**0.36**	0.19	-0.06	-0.06	0.28	0.20	**0.61**	**0.45**
Al_s	**-0.64**	**-0.47**	-0.11	-0.08	**-0.75**	**-0.60**	-0.07	-0.08
Fe_s	**-0.44**	**-0.37**	0.11	0.04	**-0.72**	**-0.54**	0.31	0.26
S_s	0.33	0.20	-0.14	-0.13	-0.23	-0.23	**0.59**	0.33
Mn_s	-0.05	-0.02	**-0.50**	-0.30	**-0.55**	-0.32	0.24	0.23
Zn_s	**-0.44**	-0.30	-0.19	-0.16	**-0.71**	**-0.58**	-0.05	-0.06

Table 3.5. Identification of vegetation groups. Different capital letters following variable values indicate significant differences between vegetation groups ($\alpha = 0.05$). Variables are defined in Table 2.1.

Vegetation group	Elevation	Ca_s	K_s	Mn_d
	Mean (95 % confidence limits)			
	(m)	(mg/kg soil)	(mg/kg soil)	(μg/10 cm^2/6weeks)
Juniper	1784B (1520, 2013)	3937A (2629, 5509)	41A (36, 48)	0.7BC (0.1, 5)
Douglas-fir	1990B (1719, 2230)	4204A (2660, 6098)	44A (37, 51)	0.2C (0, 1.5)
Subalpine fir	2396A (2207, 2571)	2627B (1582, 3935)	35B (29, 40)	4AB (0, 30)
Engelmann spruce	2625A (2497, 2748)	1528B (925, 2282)	27B (24, 31)	55A (13, 235)
Aspen	2427A (2338, 2512)	3144B (2550, 3799)	35B (32, 38)	8AB (3, 21)

Table 3.6. Identification of vegetation geo-climatic zones. Mean annual precipitation (MAP), mean annual air temperature (MAAT), mean annual soil temperature (MAST), mean summer soil temperature (MSST). Different capital letters following variable values indicate significant differences between physiognomic groups/zones ($\alpha = 0.05$). Variables are defined in Table 2.1.

Zone	Elevation	MAP	MAAT	MAST	MSST	MWST
	Mean (range)					
	(m)	(mm)	(C)	(C)	(C)	(C)
Montane	1875B (1590[a]-2285)	794B (735-917)	6.9B (5.1-8.0)	7.1B (5.9-7.8)	13.6B (11.6-14.6)	2.7A
Subalpine	2544A (2070-3060[b])	1021A (847-1137)	3.9A (3.0-6.1)	5.0A (4.2-6.6)	10.2A (8.8-12.7)	2.7A
Aspen	2426A[c] (1810-2750)	971A[c] (779-1121)	4.5A[c] (3.1-7.2)	5.4A[c] (4.3-7.3)	10.9A[c] (9.0-13.8)	2.7A

Zone	Ca_s	K_s	Mn_d	Parent material	Prevailing soil type[d]
	Mean (95 % confidence limits)				
	(mg/kg soil)	(mg/kg soil)	(µg/10 cm^2/6weeks)		
Montane	4050A (3009, 5247)	42A (38, 47)	0.4B (0.1, 2)	Fluvio-colluvial deposits	Pachic Argixerolls Typic Argixerolls
Subalpine	1894B (1332, 2553)	30B (27, 33)	22A (7, 75)	Glacial deposits Tertiary sediments	Typic Haplocryalfs Eutric Haplocryalfs
Aspen	4050A (2543, 3808)	35B (31, 38)	8A (3, 22)	Glacial deposits, fluvio-colluvial deposits, tertiary sediments, quartzite	Pachic, Typic Palecryolls Typic Argicryolls Typic Haplocryolls

[a] Elevation of the lowest point of the research area; the montane zone can spread lower

[b] Elevation of the highest point of the research area; the subalpine zone can spread higher

[c] Significant difference from the montane zone because no aspen-dominated sites sampled in the lowest elevations

[d] See Appendix A

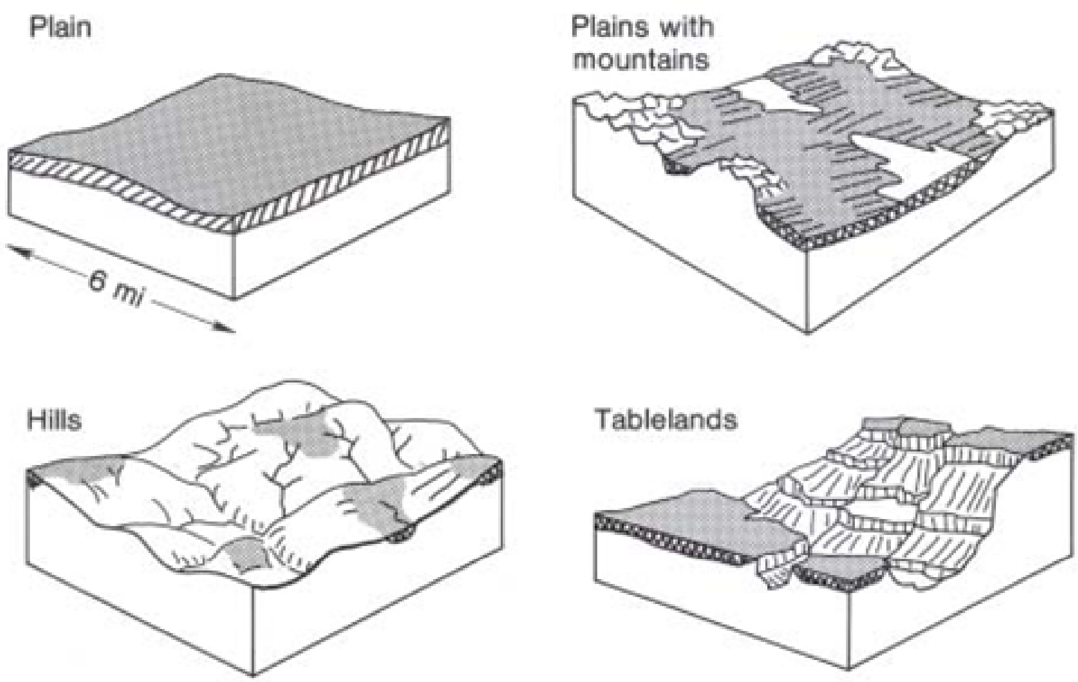


Figure 3.1. The zonal (climatic-climax) concept. Shaded areas, indirectly related to the study area, correspond with zonal sites in different types of a landscape (Bailey 1988).

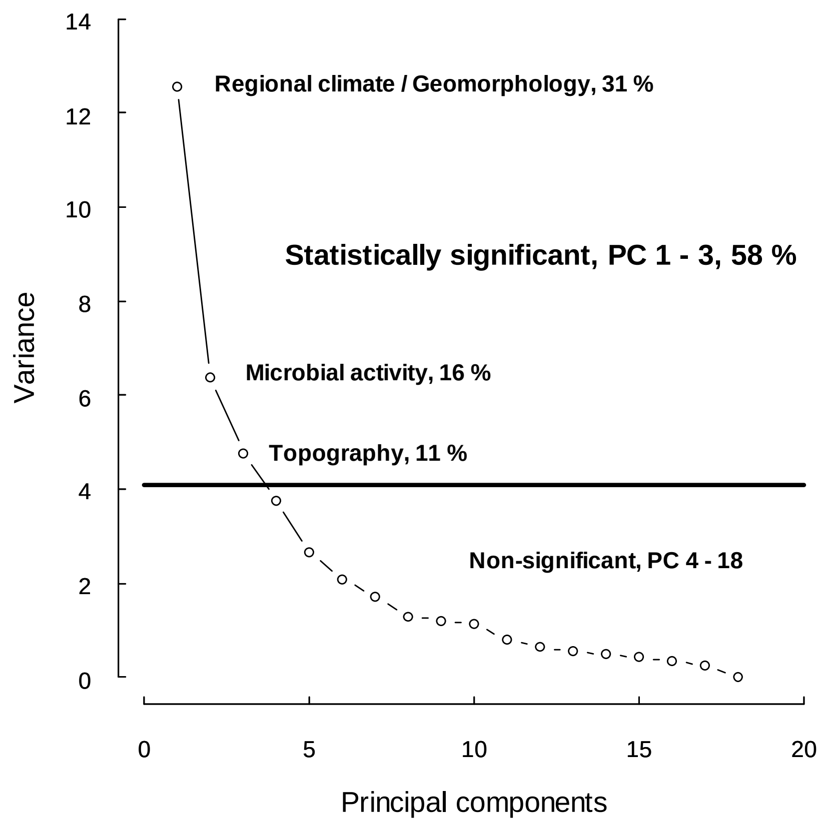
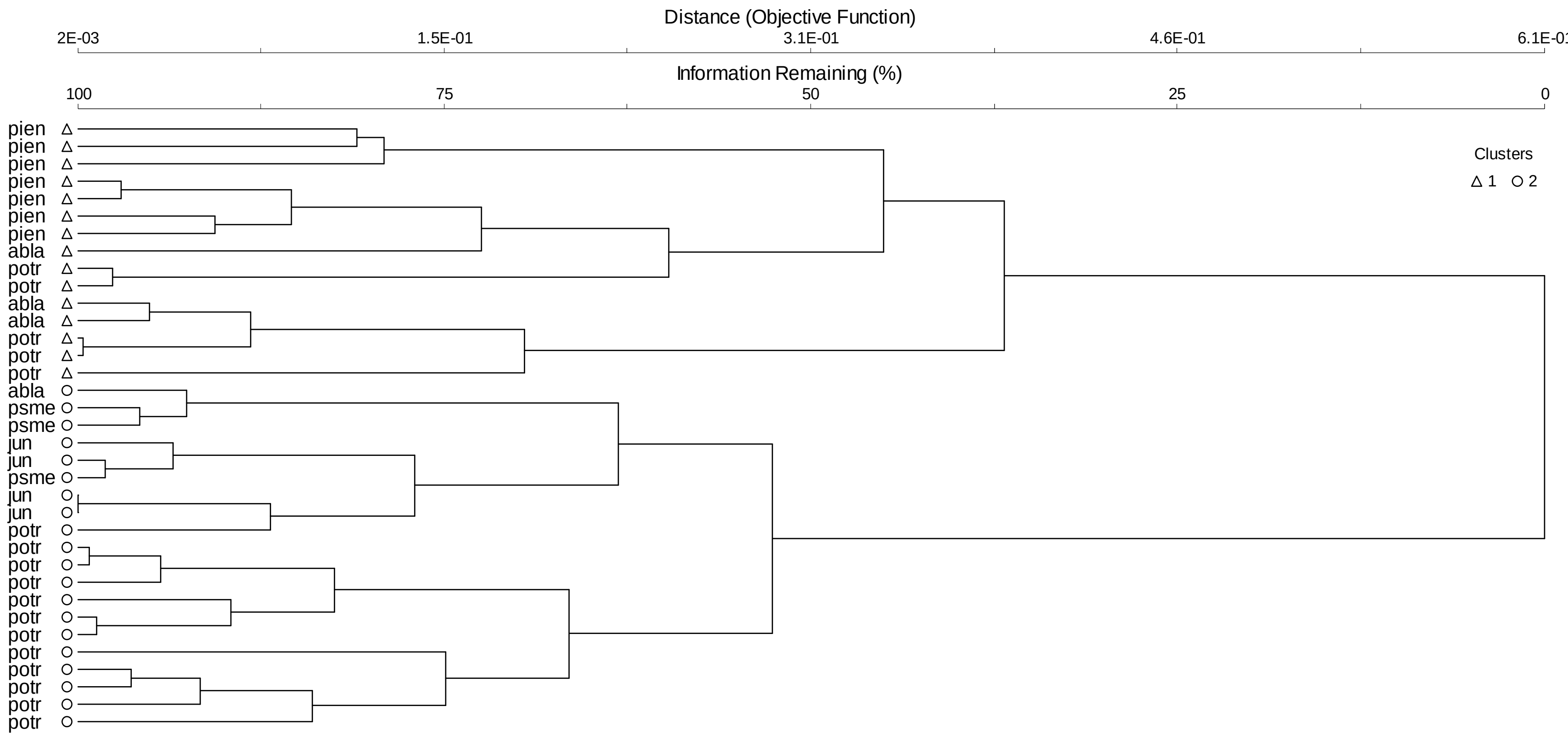


Figure 3.2. PCA scree plot on the conifer dataset. Significance and interpretation of the principal components. See text for explanation.

a



Distance (Objective Function)
2E-03
1.5E-01
3.1E-01
4.6E-01
6.1E-01
Information Remaining (%)
100
75
50
25
0
Clusters
△ 1 ○ 2
pien
pien
pien
pien
pien
pien
pien
abla
potr
potr
abla
abla
potr
potr
potr
abla
psme
psme
jun
jun
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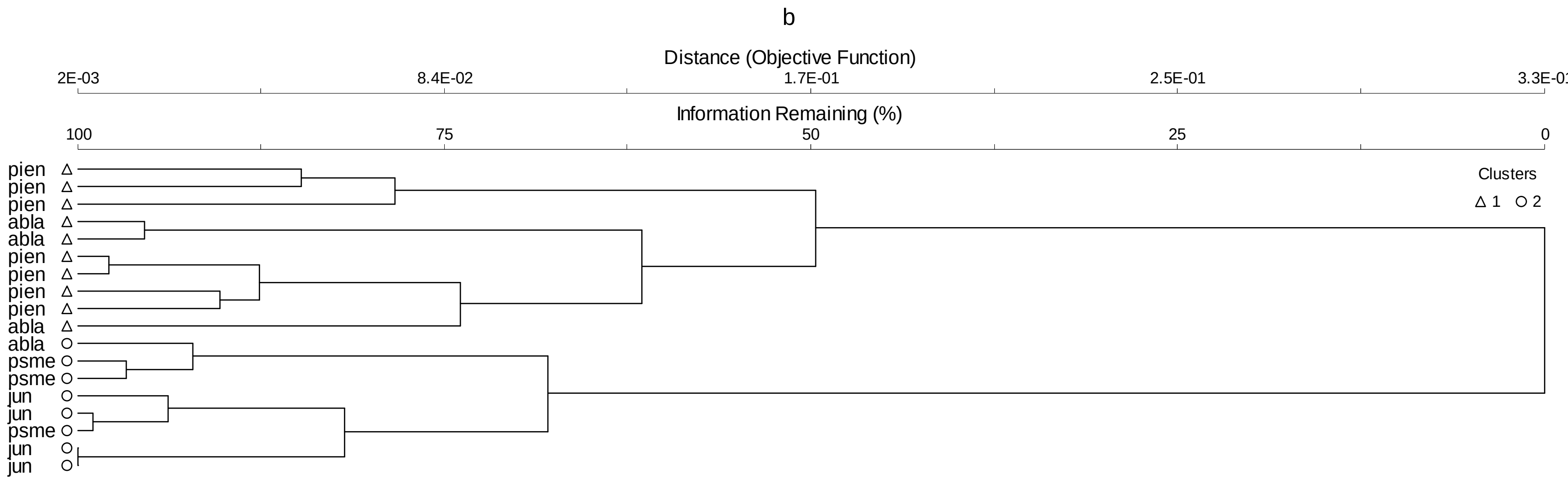

Figure 3.3. Cluster analysis dendrograms with the two cluster solution: a) the entire dataset including aspen-dominated sites; b) the conifer dataset. Rocky Mountain juniper (jun), Douglas fir (psme), aspen (potr), subalpine fir (abla), Engelmann spruce (pien) vegetation group.

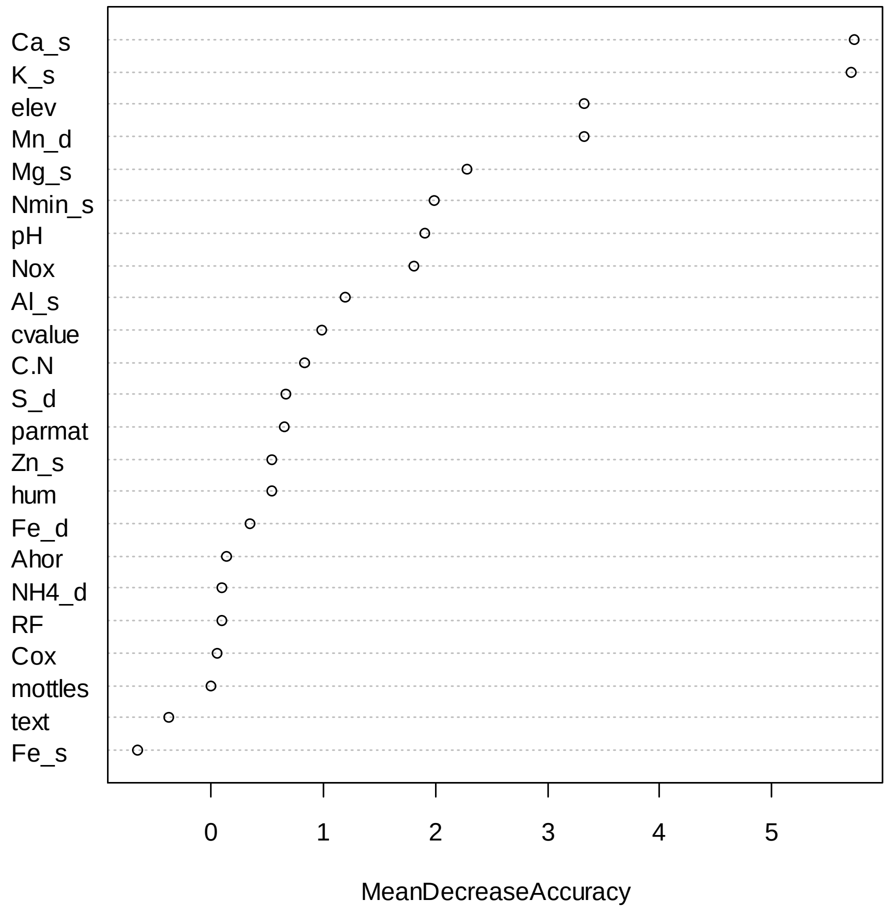

Figure 3.4. RandomForests analysis with variable importance order. Variables are defined in Table 2.1. See text for explanation.

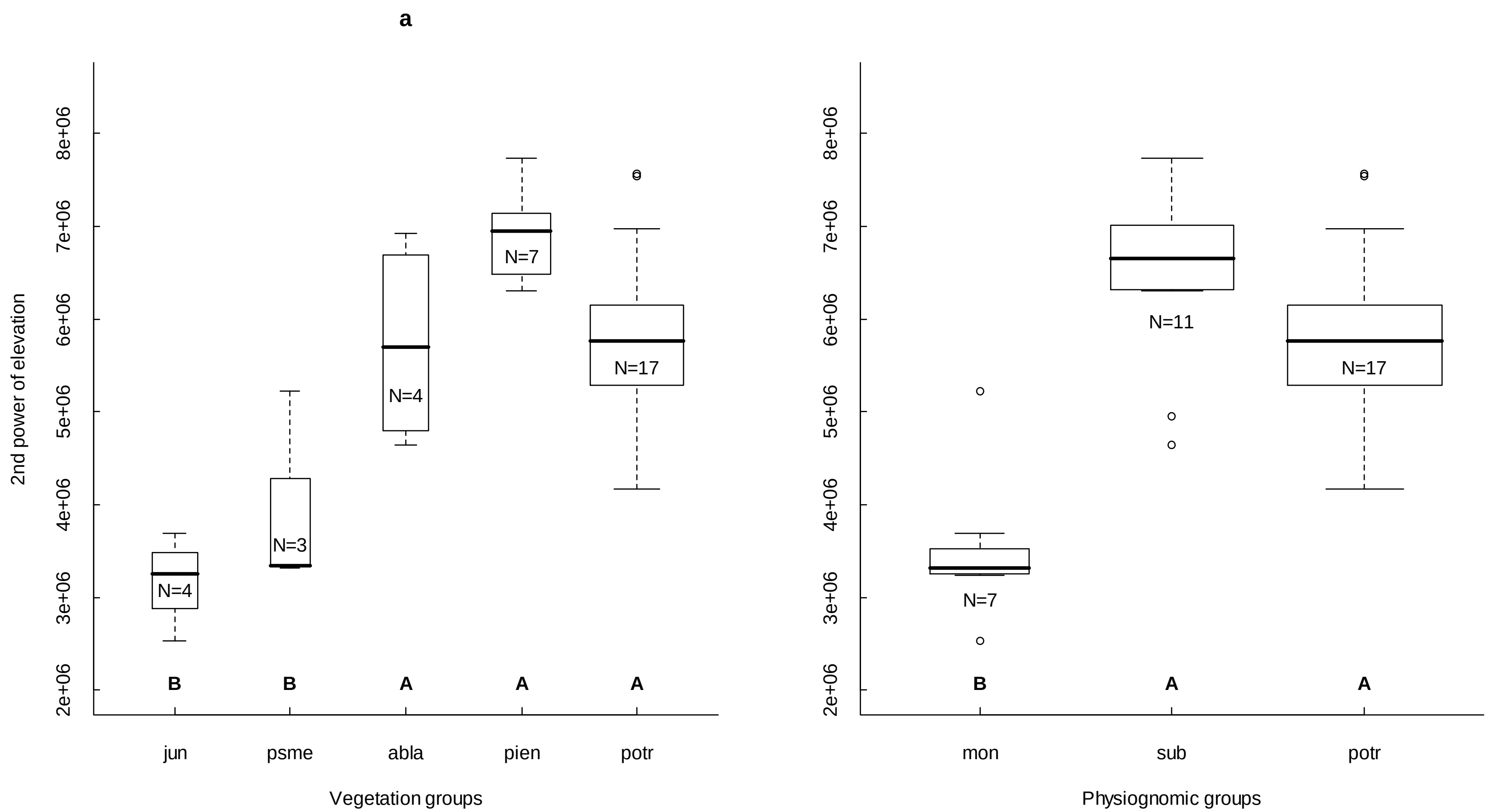

Figure 3.5. Relationship of vegetation and physiognomic groups with elevation. Different letters represent significantly different groups ($\alpha = 0.05$). Vegetation groups are defined in Fig. 3.3. See text for details.

CHAPTER 4

DIAGNOSTIC SPECIES AND FIDELITY CONCEPT IN VEGETATION CLASSIFICATION IN THE ROCKY MOUNTAINS, NORTHERN UTAH [3]

Abstract

The concept of diagnostic species and fidelity has been frequently used in European phytosociology. Based on these concepts, a statistical rather than intuitive approach was used to develop a vegetation classification in a mountainous study area in the Rocky Mountains of northern Utah.

This classification was derived from sampling of forest (spruce-fir, Douglas-fir, aspen, juniper and mahogany woodland) and non-forested (willow-riparian, low shrublands, tall-forb meadows, and sparse vegetation) ecosystems. One-hundred and fifty-seven vegetation sample plots were described by vascular plant species composition and basic habitat physiographic features (elevation, landform, slope, aspect, parent material).

Hierarchical cluster analysis reduced the original number of vegetation samples (relevés) to thirty-four meaningful vegetation units. For each species, fidelity and constancy were calculated and diagnostic species were identified for the vegetation units at the floristic level of alliances and associations, and then compared with indicator species of extensive habitat type classification in the central Rocky Mountains. Diagnostic species may have greater descriptive power than indicator species and potential value for a comprehensive ecosystem classification.

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[3] Coauthored by Antonin Kusbach, James N. Long, and Helga Van Miegroet

Introduction

"Without classification there can be no science of vegetation" - R. F. Daubenmire

Vegetation is together with animals, microbes and physical environment (i.e., climate and soils referred to hereafter as a habitat or site) a component of ecosystems of whatever size (Fosberg 1967, Pojar et al. 1987). As a distinctive landscape feature, vegetation was a fundamental component of land classifications (Daubenmire 1989). Recently, vegetation classification has become important as a communication tool in ecological research and in application of ecological information in planning, monitoring, conservation and management (Jennings et al. 2009).

Early land and vegetation classifications in the western U.S. such as the concept of potential natural vegetation (Küchler 1969) and habitat types (Daubenmire 1952), were based largely on constancy and dominance of species occurring in potential climax communities using the classic Braun-Blanquet method of sorting of phytocoenological tables. The most frequent and dominant species were considered indicators of vegetation units. This approach stressed species' abundance regardless of their presence in other vegetation units; and while quantitative, it was intuitive, and not statistical (Chytrý et al. 2002a). A statistical approach, on the other hand, accounts for the relationship between the number of unique vegetation samples (relevés) in vegetation units and in the total data set (Barkman 1989). This promising approach is associated with the concepts of diagnostic species (Whittaker 1962, Westhoff and van der Maarel 1973, Jennings et al. 2008, 2009) and the concept of fidelity (Chytrý et al. 2002a). Some approaches to the concept of diagnostic species are stricter (e.g., European), constrained to character species (i.e., species occurring in a single vegetation unit for which it is characteristic) and differential species (i.e., species occurring in a few vegetation units which they discriminate) (Mueller-Dombois and Ellenberg 1974, Bruelheide 2000, Chytrý et al. 2002a). Alternatively, some approaches apply a looser interpretation, including also constant species (i.e., the most frequent) and dominant species (i.e., species with high cover) (Westhoff and van der Maarel 1973, Brohman and Bryant 2005, Winthers et al. 2005, FGDC 2008, Jennings et al. 2008, 2009).

Fidelity is a measure of species concentration, (*sensu* Chytrý et al. 2002a) in vegetation units. It is based on species' frequencies observed within a vegetation unit compared with expected frequencies if the species' distributions were random, i.e., taking also out-of-unit species occurrence into consideration (within a total data set) (Barkman 1989, Chytrý et al. 2002a). Fidelity is thus a measure of species-unit association. In contrast, constancy as a usual and more common measure of species frequency in vegetation units in the past, does not take into consideration species outside its primary vegetation unit. It has been suggested that the use of fidelity relative to diagnostic species may increase the general validity of vegetation types in large phytosociological data bases representing broad taxonomic units such as orders or classes, and also in smaller data sets representing a geographically small but diverse area (with large ecological variation) (Chytrý et al. 2002a).

There are two major tasks in vegetation classification: (1) to distinguish meaningful (i.e., interpretable) groups of species within the original dataset and thereby reducing the number of relevés to a fewer number of more or less similar and meaningful **vegetation units**; and (2) to identify **diagnostic species** within these vegetation units.

We used the fidelity concept to analyse vegetation in the study area representing the

Rocky Mountains, northern Utah. Diagnostic species were not identified intuitively based on subjective constancy and dominance thresholds. Rather they were identified based on fidelity calculations, a more objective and statistical approach. We expect to reveal a descriptive power of diagnostic species and introduce meaningful vegetation units and therefore, a better understanding of vegetation patterns, particularly the distribution of species assemblages in the Rocky Mountains of northern Utah. Our specific objectives are to: (1) perform an objective classification based on specification of feasible vegetation units; and (2) identify species diagnostic of particular vegetation units and potentially useful for recognition of these vegetation units in the study area.

Methods

Study area

Franklin Basin and the T.W. Daniel Experimental Forest make up the study area (ca 16,000 ha, and ca 1,000 m of vertical extent) (Fig. 2.2). Franklin Basin (FB, 15,000 ha) is a montane-subalpine area situated between the Bear River Range and the Wasatch Range in the central Rocky Mountains on the Utah and Idaho border. The T.W. Daniel Experimental Forest (TWDEF, ca 1000 ha) is situated on a high ridge plateau of the Wasatch Range (10 km to the southeast of FB).

According to Bailey (1998) and McNab et al. (2007), the study area occurs within M331 Southern Rocky Mountains Steppe-Open Woodland-Coniferous Forest-Alpine Meadow Province, “D” Overthrust Mountain Section, “n” Northern Wasatch Range, and “o” Bear River Front Range Subsections. The mean total annual precipitation ranges from 720 to 1250 mm and mean annual air temperature ranges from 2.4 to 5.7 ^{o}C for

Temple Fork, Tony Grove Lake, Franklin Basin, and Utah State University (USU) Doc Daniel weather stations (http://www.wcc.nrcs.usda.gov/snow/).

The terrain is mountainous, rocky and steep with occasional flat to gently sloping high ridge-plateaus and benches. The elevation ranges from 2050-3060 m across the two study sites. The highest area of the Bear River Range was glaciated during the Pleistocene as manifested by glacial geomorphologic features like moraines, U-shaped valleys, erratics, and irregular glacial deposits (Atwood 1909, Young 1939, Degraff 1976). The study area is mostly built from calcareous sedimentary rocks (limestone, dolomite) with interlayered quartzite, and from Tertiary sediments consisting of grit, conglomerate, and siltstone of the Wasatch Formation at the TWDEF site. The soils are formed in residuum, colluvium, alluvium, glacial till and outwash, and occur on diverse landforms such as cliffs, talus slope, moraines, karst valleys, mountain slopes, landslides, plains, valleys, depressions, ravines, and wetlands (Schoeneberger et al. 2002).

Over half of the study area is occupied by forest ecosystems including Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), and woodland ecosystems including mountain mahogany (*Cercocarpus ledifolius*) and Rocky Mountain juniper (*Juniperus scopulorum*). Substantial changes in fire regimes, often in combination with cutting and grazing, have led to dramatic changes in the structure and the age-class distribution of forest stands. In many places, 100- to 140-year-old stands are now predominant (Long 1994). Forests in the study area are thus characterized by mid- and late-seral stages where forest understory is usually well developed (Pfister and Arno 1980). Non-forested ecosystems include willow-riparian (*Salix spp.*) and wetlands, low shrublands (*Artemisia* *spp.*), tall-forb meadows, and sparse vegetation on talus and rock outcrops, which may represent stable or temporary communities. Despite human impacts in last 120 years, the study area is considered relatively natural in terms of plant species composition (Bird 1964).

Data collection

We collected vegetation data (relevés) on 157 sample plots across the study area in the summers (late May-August) of 2006 and 2007. Sampling followed the Existing Vegetation Classification and Mapping Technical Guide (Brohman and Bryant 2005), and Terrestrial Ecological Unit Inventory Technical Guide (Winthers et al. 2005). After field reconnaissance, we sampled vegetation across a broad range of the physical environment in order to capture as much environmental variation as possible. In an effort to minimize the major influence of historical factors such as fires and logging and stress the impact of the physical environment on vegetation, we focused on mature, late-successional, and relatively stable plant communities. In the case of forest vegetation, this condition was characterized by advance regeneration of potential climax tree species (Pfister and Arno 1980, Pojar et al. 1987). We sampled stands reasonably uniform in physiognomy, floristic composition and environment (Jennings et al. 2009). We avoided ecotones, i.e., habitats in transition, where important environmental factors merge, as well as degraded or atypical stands. Because 6 sample plots did not fulfill these conditions entirely, they were excluded from the original scheme of 163 sample plots described in earlier chapters. A stratified (based on vegetation physiognomy) fixed (subjective selection) sampling design was used with sample plot size of 1000 m^2 for forest and 100 m^2 for non-forested ecosystems and three replicates were considered the minimum for defining a preliminary vegetation unit (Podani 2000, Brohman and Bryant 2005, Jennings et al. 2009). The plots were usually circular, but the shape was adjusted according to the character of habitat, e.g., linear for riparian vegetation. Each sample plot was described by complete enumeration of vascular plant species abundances (canopy cover percentage for forest and ground cover percentage for forest and non-forested understory), strata (trees, shrubs, and understory), and by basic habitat (site) physiographic characteristics (e.g., elevation, slope, aspect, landform, parent material).

Data analysis

Vegetation analysis followed the Existing Vegetation Classification and Mapping Technical Guide (Brohman and Bryant 2005), the National Vegetation Classification Standard (FGDC 2008), and Standards for Associations and Alliances of the U.S. National Vegetation Classification (Jennings et al. 2009). We ran an analysis of the 157 relevés representing 327 species (Appendix B).

There were two steps in the analysis: (1) partitioning of the dataset into meaningful vegetation units/clusters; and (2) characterization of vegetation units based on diagnostic species.

To partition the community data we used two common approaches, represented by agglomerative and divisive methods. The agglomerative approach involved hierarchical clustering with Ward's and Flexible beta linkage methods combined with Euclidean and Sørensen distance measures (Bray and Curtis 1957, Ward 1963). Percentage cover was standardized by both logarithmic and less drastic square root transformations. The divisive approach was represented by Modified TWINSPAN, which prevents unsubstantiated division of homogeneous clusters (Roleček et al. 2009). Here, we applied three measures of within-cluster heterogeneity: Whittaker's beta (Whittaker 1960); total inertia (Greenacre 2000); and chord distance (Orlóci 1967). We deleted rare species with just one occurrence in the entire dataset before partitioning the dataset.

Using both the agglomerative and divisive approaches, nine alternative partitioning methods were assessed by OptimClass. It is a method for identifying the optimal partitioning of a set of relevés (Tichý et al. 2009). In OptimClass, for each partitioning method, the total number of faithful species was calculated by Fisher's exact test as a measure of species-to-unit fidelity for presence/absence data (Chytrý et al. 2002a). The best partitioning method was chosen from all solutions based on the total number of faithful species and interpretability of vegetation units. This best solution was thus a compromise between statistical assessment represented by Fisher's exact test and ecological feasibility represented by meaningful, i.e., interpretable vegetation units (Chytrý et al. 2002a). We removed small-member clusters, i.e., vegetation units represented just by one and two relevés within the best partitioning solution because small units created at high hierarchical levels are considered outliers (Tichý et al. 2009, McCune and Grace 2002, Jennings et al. 2009); they could be either undersampled or rare in the study area. Finally, we repeated the partitioning for the best method, i.e., we achieved the appropriate number of vegetation units/clusters based on interpretability, size of vegetation units and the number of faithful species.

We used fidelity calculation to determine faithful species in the second step of the analysis with the expectation that this method should improve the general validity of vegetation types. There are many measures of fidelity such as *u* value (Bruelheide 2000), chi-square statistic, G statistic, Fisher's exact test and Indicator Value Index (Dufrêne and Legendre 1997); we used **phi coefficient** of association (Sokal and Rohlf 1995). In common in other fidelity measures, it is based on comparison of observed/expected frequencies, i.e., probability of species' non-random occurrence (Chytrý et al. 2002a). The main advantage of this coefficient is that it is, unlike other fidelity measures, independent of the size of the dataset (the number of relevés in the dataset); therefore, it is useful to compare species fidelities among differently sized datasets and vegetation units (Chytrý et al. 2002a). The phi coefficient value ranges from -1 to +1(-100 to +100 %) with positive value indicating the species-unit co-occurrence is more often than expected by chance only. If the species is completely faithful to the unit the value is 1 (100 %) (Chytrý et al. 2002a).

To minimize possible effects of unequal-sized vegetation units, we calculated the phi coefficient with presence/absence data after standardization of the units' size (number of relevés) (Tichý and Chytrý 2006). Species presence/absence provides a better fidelity measure than cover abundance because it is less affected by high fluctuations of species cover and observer bias (Chytrý et al. 2002a). Statistical significance of the phi coefficient was assessed by Fisher's exact test with $p < 0.05$.

There is no fixed threshold for the phi coefficient. We set a threshold of phi > 40 % for faithful species. A higher threshold would be too restrictive producing a low number of faithful species. Conversely, a lower threshold would produce an unnecessarily large number of 'faithful' species with limited diagnostic power in this relatively small dataset. Diagnostic species were defined based on the following thresholds: faithful species, phi >

40 %; constant species, constancy (frequency) > 60 % (Mueller-Dombois and Ellenberg 1974); and dominant species, cover > 5 % This relatively low cover value was chosen in light of sparse communities such as woodland and high elevation open-canopy conifer forests that would be otherwise underestimated compared to thick forest communities. Character species were all faithful species (with phi > 40 %) occurring in a single vegetation unit only and thus highly faithful to it. Differential species were all faithful species occurring in a few vegetation units; in fact, these species discriminate these units.

As analysis outputs we created: (1) an **advanced combined synoptic table**; and (2) an **analysis of synoptic table** where diagnostic species are explicitly listed. In the advanced combined synoptic table, species were sorted by the phi coefficient threshold value (phi > 40 %). This fidelity information was combined and compared with constancy (frequency) value. Both the advanced combined synoptic table and analysis of synoptic table are available as an automatic procedure in the JUICE program (Tichý 2002).

The relationship among vegetation units and “goodness” of each unit was based on number of faithful species and the average positive fidelity calculated as a simple mean of non-negative fidelity values. We also calculated species richness as a simple number of species within a vegetation unit and an indicator of local (alpha) species diversity (e.g., Whittaker 1972, McCune and Grace 2002, Colwell et al. 2004). But this diversity measure should be considered with caution because it is highly dependent on the number of relevés (Gotelli and Colwell 2001, Colwell et al. 2004). We considered good, i.e., well defined, units as those with three and more faithful species and high average positive fidelity (> 30 %). Weak, i.e., poorly defined, units were those with few or no faithful species and low average positive fidelity (< 30 %) (Chytrý et al. 2002a).

Based on these outputs, we proposed vegetation types as species assemblages at the floristic level of vegetation alliances and associations (Grossman et al. 1998, FGDC 2008, Jennings et al. 2008, 2009). Alliances were suggested as compilations of diagnostic species which are differential and constant (frequent), and with particular preference for tree species (FGDC 2008, Jennings et al. 2009). Associations were suggested as compilations of character species. In the case of a weak (poorly defined) vegetation unit, because no faithful species were present, the most constant (frequent) and dominant species were considered as diagnostic.

JUICE software version 7. 0. 48. (Tichý 2002) and PC-ORD 5 (McCune and Mefford 2006) were used in the partitioning analysis. Diagnostic species within vegetation units were analyzed using JUICE.

Results

Partitioning the dataset

The more relevés in a vegetation unit the better that unit may be defined. Especially in the case of our small dataset we expected greater descriptive power of diagnostic species inside larger vegetation units than in small units (less than three relevés) where there was a greater possibility of faithful species presence solely by chance. Therefore, when appropriate, we opted for larger vegetation units. Using OptimClass, we chose the partitioning based on Ward/Euclidean/square root transformation as the best of the nine alternative solutions. It retained both a high total number of faithful species (395) and relatively large units (32). In contrast, the Ward/Sørensen solution provided the highest number of faithful species (403) but also detailed clustering representing 48 vegetation units, some of which were relatively small and potentially weak (Fig. 4.1). The flexible beta and Modified TWINSPAN solutions did not produced as many faithful species as Ward/Euclidean clustering (e.g., Brown 2006).

The repeated division after the removal of small-member clusters, i.e., vegetation units represented just by one and two relevés within the best partitioning solution, resulted in the appropriate partitioning into 34 vegetation units. These units were readily interpretable and had meaningul size related to the size of the entire data set. Additional division yielded units that were too small; they became less interpretable despite the higher number of faithful species.

Characterization of vegetation units

The advanced combined synoptic table displayed differences within and between the vegetation units. Species were sorted by decreasing fidelity at the phi coefficient positive threshold value (phi > 40) into diagonally arranged blocks (Tichý 2002). Fidelity values were complemented by constancy/frequency values (Appendix C). It is obvious that consistency between fidelity and constancy was not perfect. Rather, species with high fidelity did not inevitably have high constancy and species completely constant were not necessarily faithful. This was true for the majority of tree species and, for example, some undergrowth species such as *Osmorhiza chilensis*, *Pedicularis racemosa* and *Berberis repens*, important indicator species in habitat typing.

The diagonal blocks, unique for each vegetation unit, consisted of character species. Additionally, more or less regular blocks or single faithful species lower in the synoptic table occurring in a few vegetation units, represented differential species. This sorting helped to distinguish character and differential species and together with the analysis of synoptic table facilitated characterization of the vegetation units by diagnostic species (Appendix D). Potential alliances and associations were identified for all units with short description of the habitat. Table 4.1 includes forest (conifer and broad-leaved) and woodland (conifer and broad-leaved) vegetation units; Table 4.2 includes non-forested/ rangeland (shrubland, dwarf-shrubland, herbaceous and sparse vegetation) vegetation units (Lund 2006, Grossman et al. 1998, FGDC 2008). Habitat characterization of the vegetation units was based on simple physiographic factors and elevation stratification relative to the elevation range within the study area: low elevation < ca 2350 m; high elevation 2350-2650 m; subalpine 2650-2950 m; alpine > 2950 m.

Some species were present in the majority of vegetation units, e.g., *Symphoricarpos oreophilus, Thalictrum fendlerii, Osmorhiza chilensis, Paxistima myrsinites*. In contrast to these generalists, other species appear to be habitat specialists, as they were restricted to as few as two units. e.g., *Zigadenus elegans, Cercocarpus ledifolius, Juniperus scopulorum*. Interestingly, several tree species appear in the majority of forest vegetation units and showed a high degree of coexistence, e.g., *Picea engelmannii* with *Abies lasiocarpa* or *Populus tremuloides* with conifers (Appendix C, D).

Of the 34 vegetation units, 23 were good (well defined) having three and more faithful species and the average positive fidelity greater than 30. Eleven units were weak (poorly defined) with less than three faithful species and the average positive fidelity less than 30. The average species richness of weak groups was 62.3 whereas the richness of good groups was 51.8. Aspen units appeared to be somewhat weak (the average species richness 66.3) except the unit on wet habitat (vegetation unit 20, species richness 43) (Appendix C, Table 4.1, 4.2).

Discussion

Interpretation of classification

The good and weak vegetation units were associated with interesting patterns which may facilitate their explanation and interpretation. For example, based on habitat description (Table 4.1, 4.2), the good units were associated with extreme environments such as wet, rocky, or strongly calcareous sites. In contrast, the weak units were associated with moderate environments such as well drained, non-skeletal sites on moderately deep soils. The distribution of those species which we interpret to be site specialists appeared to be driven by environmental factors such as soil moisture and pH, whereas occurrence of site generalists may be explained by spatial/temporal factors, such as dispersal processes and patch dynamics (Pandit et al. 2009). Additionally, vegetation units in intermediate environmental conditions tended to have greater species richness represented by mostly habitat generalists and fewer specialists (Hájek et al. 2007). For example, units 1, 2, 20, 32, 33, 34 (Table 4.1, 4.2) with wet conditions and units 10, 11, 12, 27, 28 with dry calcareous conditions had the highest number of faithful species as potential specialists and relatively low species richness whereas the units 3, 6, 16, 17, 18, 19, 21, 22, 23 with intermediate environmental conditions had few or no faithful species but high species richness mostly consisting of generalists.

In the study area, habitats with intermediate environmental conditions (e.g., slightly undulating or flat terrain, moderate-deep soils, little or no rocks) tend to be accessible and, therefore, potentially subject to greater human-caused disturbances such as logging and domestic livestock use. In general, disturbed sites probably have fewer site specialists and many common species (Gaublomme et al. 2008). This characterization is consistent with our data; accessible, presumably more highly disturbed sites do in fact support a richness of site generalists and a low number of specialists that may reflect site history, e.g., grazing in past 120 years (Appendix C, Table 4.1, 4.2) (Hájek et al. 2007, Pärtel et al. 2001).

The 11 weak units may reflect the challenge associated with sampling special habitats. In some cases it was difficult to avoid ecotones, for example, riparian vs. valley bottom transition (unit 3), and delineate a real mosaic of narrow corridors affected by high ground water table. Another example is a dry habitat of cliffs with inter-layered benches (unit 31), resulting in a sample representing a mosaic of rocks and deeper soil. Additionally, in the case of high-elevation open-canopy spruce-fir forest, typical forest species were described together with species typical of non-forest vegetation units. Because we analyzed both forest and non-forested ecosystems together, “goodness” of these high-elevation forest units could be affected by difficulties connected to separation of forest from non-forested vegetation units (e.g., units 3, 8, 9).

Finally, dataset size may over-emphasis or strengthens the ‘goodness’ of vegetation units; some units appear to be good in our dataset but their status might change with spatial expansion of the sampling, likely resulting in an increasing number of species and potential expansion of environmental conditions (Chytrý et al. 2002a). Listed faithful species should be interpreted with caution and within the context of this study, but we assume they may represent regional character or differential species (Willner 2001, Chytrý et al. 2002a). The diagnostic species were interpreted for a relatively narrow geographical area, yet covered a broad environmental range. Therefore, we suggest this local geographical context may be close to regional (e.g., Chytrý et al. 2002b).

Potential value of classification

The most extensive vegetation classifications of forests in the central Rocky Mountains were based on habitat and community typing (e.g., Daubenmire 1952, Pfister and Arno 1980, Mauk and Henderson 1984, Mueggler 1988). Habitat and community type analyses did not include woodland and riparian plant communities in contrast to our classification which includes a much broader range of vegetation types, including non-forested communities.

In these earlier classifications, indicator species were both highly constant and dominant within a particular vegetation unit (habitat or community type) and their selection was subjective and largely quantitative. Moreover, looking at the distribution of these indicators more closely reveals that they do not occur only inside one habitat/community type (e.g., *Berberis repens*, *Osmorhiza chilensis* and *Pedicularis racemosa* habitat types of *Pseudotsuga menziesii*, *Picea engelmannii* and *Abies lasiocarpa* series) but also across habitat series (e.g., consider *Picea engelmannii* and *Abies lasiocarpa* occurrence throughout these series). Consequently, these habitat/community type indicator species may not be useful in discriminating between environmental conditions. Our analysis revealed faithful species different from indicator species of habitat/community types. We assume that faithful (character or differential) species are better vegetation unit descriptors than common and abundant species (generalists) because they are more reflective of the underlying environment (Chapter 5).

In the case of the weak units (i.e., conifer units 3, 6, 9; aspen units 16, 17, 18, 19; and shrubland units 21, 22, 23, 31) additional research is needed to decide if sampling was appropriate. For example, classification of environmentally intermediate aspen communities is difficult using the fidelity and diagnostic species approach. Because of generally rich understory cover, and presence of many generalists in contrast to few species with high fidelity, ecotones between aspen units are both abundant and ambiguous. This vast floristic variability of aspen units is consistent with exclusion of aspen communities from vegetation geo-climatic zonation because of their environmental amplitude (Chapter 3) and their not always clear successional status (Mueggler 1988). We suspect a more detailed environmental description and sampling of aspen habitat (e.g., pH of soils or nutrient characteristics) might lead to better vegetation discrimination of aspen units.

Our vegetation classification revealed that major tree species such as Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*), limber pine (*Pinus flexilis*) and aspen (*Populus tremuloides*) appear in a high degree of coexistence with other tree species (Appendix C, D). This finding is consistent with vegetation geo-climatic zonation (Chapter 3).

Summary and conclusions

Using the concept of diagnostic species and fidelity, we created a vegetation classification based on vegetation sampling of the floristically and environmentally complex study area in the Rocky Mountains of northern Utah. Based on cluster analysis of a community data set, we identified thirty-four vegetation units. For each species, fidelity and constancy was calculated. Then, diagnostic species were determined for each vegetation unit at the floristic level of alliances and associations.

We compared our approach with habitat and community type classification in the central Rocky Mountains. We suggest that: (1) strict separation of tree species is unsubstantiated from a classification standpoint; (2) diagnostic species are more strongly associated with their underlying physical environment than indicator species *sensu* habitat type; and (3) our vegetation classification results from complex analysis of existing vegetation in broad range of ecosystems (forest, woodland, riparian, non-forested).

Any taxonomic classification based strictly on vegetation is somewhat limited in ecological interpretations. Ultimately, both vegetation and the physical environment should be included as a part of a comprehensive ecosystem classification.

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Table 4.1. Forest and woodland vegetation units, proposed alliance and association compilations and habitat description.

Unit	Alliance	Association	Label	Habitat
1	*Abies lasiocarpa*	*Galium boreale*	Abla-Pien/Gabo	Low elevation riparian
	Picea engelmannii	*Potentilla gracilis*		
	Angelica arguta	*Epilobium ciliatum*		
	Lonicera involucrata	*Potentilla fruticosa*		
	Salix boothii	*Salix bebbiana*		
2		*Zigadenus elegans*	Abla-Pien/Ziel	High elevation wetlands
		Aconitum columbianum		
		Salix wolfii		
		Pedicularis groenlandica		
		Senecio triangularis		
3	*Abies lasiocarpa*	*Thalictrum fendleri*	Abla-Pien/Thfe	High elevation conifer valley bottoms
	Picea engelmannii	*Pedicularis racemosa*		
	Arnica cordifolia	*Rudbeckia occidentalis*		
		Ligusticum filicinum		
		Osmorhiza chilensis		
4		*Lonicera utahensis*	Abla-Pien/Lout	Subalpine shady slopes
		Ranunculus jovis		
		Arnica latifolia		
		Pyrola secunda		
		Aster occidentalis		

Unit	Alliance	Association	Label	Habitat
5	*Abies lasiocarpa*	*Ligusticum porteri*	Abla-Pien-Potr/Lipo	Subalpine undulating plateaus
	Picea engelmannii	*Poa bolanderi*		
	Populus tremuloides	*Hieracium albiflorum*		
		Osmorhiza chilensis		
		Ligusticum filicinum		
6		*Osmorhiza chilensis*	Abla-Pien-Potr/Osch	Undulating glacial moraines
		Rudbeckia occidentalis		
		Thalictrum fendleri		
		Pseudotsuga menziesii		
7	*Abies lasiocarpa*	*Rubus parviflorus*	Abla-Pien-Psme/Rupa	High elevation shady skeletal slopes
	Picea engelmannii	*Goodyera oblongifolia*		
	Pseudotsuga menziesii	*Sorbus scopulina*		
	Carex geyeri	*Chimaphila umbellata*		
		Pyrola secunda		
8		*Rubus idaeus*	Abla-Pien-Psme/Ruid	Quartzite talus
		Juncus parryi		Sparse vegetation
		Poa cusickii		
9	*Abies lasiocarpa*	*Anemone multifida*	Abla-Pien-Pifl/Anmu	Subalpine rocky calcareous slopes/flats
	Picea engelmannii	*Thlaspi montanum*		
	Pinus flexilis	*Pedicularis racemosa*		
	Pseudotsuga menziesii	*Aster engelmannii*		
		Penstemon leonardii		

Unit	Alliance	Association	Label	Habitat
10	*Juniperus scopulorum*	*Lomatium grayi*	Jusc/Logr	Very dry skeletal conifer woodland slopes
	Artemisia tridentata	*Calochortus nuttallii*		
	Elymus spicatus	*Artemisia arbuscula*		
	Balsamorhiza sagittata	*Zigadenus paniculatus*		
		Ceanothus velutinus		
11	*Cercocarpus ledifolius*	*Mertensia oblongifolia*	Cele/Meob	Dry calcareous slopes
	Artemisia tridentata	*Crepis acuminata*		
	Pseudotsuga menziesii	*Viola purpurea*		
	Pinus flexilis	*Chrysothamnus viscidiflorus*		
	Elymus spicatus	*Ceanothus velutinus*		
12		*Petradoria pumila*	Cele/Pepu	Extremely dry calcareous rocks and cliffs
		Solidago nana		
		Aster ascendens		
		Comandra umbellata		
13	*Pseudotsuga menziesii*	*Acer grandidentatum*	Psme-Abla/Acgr	Low elevation shady slopes
	Abies lasiocarpa	*Arnica cordifolia*		
	Symphoricarpos oreophilus	*Smilacina racemosa*		
		Viola adunca		
14	*Pseudotsuga menziesii*	*Linanthastrum nuttallii*	Psme-Abla-Pifl/Linu	Subalpine sunny calcareous slopes
	Pinus flexilis	*Aster glaucodes*		
	Abies lasiocarpa	*Acer glabrum*		
	Juniperus communis	*Berberis repens*		

Unit	Alliance	Association	Label	Habitat
15	*Pseudotsuga menziesii*	*Astragalus tenellus*	Psme-Pifl/Aste	High elevation sunny calcareous slopes
	Pinus flexilis	*Bromus anomalus*		
	Symphoricarpos oreophilus	*Shepherdia canadensis*		
		Lomatium graveolens		
		Leucopoa kingii		
16	*Populus tremuloides*	*Poa leptocoma*	Potr-Abla-Pien/Pole	Moderate quartzite slopes
	Abies lasiocarpa	*Lupinus argenteus*		
	Picea engelmannii	*Artemisia ludoviciana*		
17	*Populus tremuloides*	*Valeriana occidentalis*	Potr-Abla/Vaoc	Toe slopes, glacial moraines, moderate slopes
	Abies lasiocarpa	*Tragopogon dubius**		
	Lathyrus pauciflorus	*Rudbeckia occidentalis*		
18		*Symphoricarpos oreophilus*	Potr-Abla/Syor	Undulating glacial moraines
		Thalictrum fendleri		
		Senecio serra		
19		*Scrophularia lanceolata*	Potr-Abla/Scla	Moderate alcaline/calcareous mid-slopes
		Valeriana occidentalis		
		Symphoricarpos oreophilus		
20	*Populus tremuloides*	*Cynoglossum officinale*	Potr/Cyof	Moist and wet valley bottoms
	Veratrum californicum	*Dactylis glomerata**		
	Carex pachystachya	*Allium bisceptrum*		
	Elymus cinereus	*Ranunculus orthorhynchus*		
		*Bromus ciliatus**		

* Introduced species

Table 4.2. Non-forested vegetation units, proposed alliance and association compilations and habitat description.

Unit	Alliance	Association	Label	Habitat
21	*Artemisia spiciformis*	*Chrysothamnus viscidiflorus*	Arsp/Chvi	Low elevation valley bottoms/slopes
	Symphoricarpos oreophilus	*Elymus cinereus*		
		Senecio serra		
		Agastache urticifolia		
22		*Poa arnowiae*	Arsp/Poar	High elevation valley bottoms/slopes
		Eriogonum heracleoides		
		Penstemon cyananthus		
		Eriogonum umbellatum		
23		*Agastache urticifolia*	Arsp/Agur	High elevation valley bottoms
		Rudbeckia occidentalis		
		Geranium viscosissimum		
		Potentilla glandulosa		
24		*Wyethia amplexicaulis*	Arsp/Wyam	Low elevation undulating moraines
		*Poa bulbosa**		
		Antennaria parvifolia		
		Poa secunda		
		Artemisia arbuscula		
25	*Rudbeckia occidentalis*	*Ranunculus adoneus*	Ruoc/Raad	Subalpine depressions/colluvial outwashes
	Ligusticum filicinum	*Carex multicostata*		
	Delphinium occidentale	*Polygonum douglasii*		
		Stipa nelsonii		
		Bromus carinatus		

Unit	Alliance	Association	Label	Habitat
26	*Agastache urticifolia*	*Aster integrifolius*	Agur/Asin	Subalpine flats/slopes
	Osmorhiza occidentalis	*Heuchera parviflora*		
	Geranium viscosissimum	*Elymus lanceolatus*		
	Helianthella uniflora			
27	*Linum kingii*	*Clematis occidentalis*	Liki/Cloc	Subalpine sunny slopes
	Linum lewisii	*Linanthastrum nuttallii*		
	Penstemon compactus	*Aster glaucodes*		
	Lomatium graveolens	*Berberis repens*		
28		*Hymenoxys acaulis*	Liki/Hyac	Alpine talus and rocks
		Phlox hoodii		Shallow soils
		Synthyris pinnatifida		
		Phlox pulvinata		
		Anemone multifida		
29	*Ivesia gordonii*	*Juncus parryi*	Ivgo/Jupa	Quartzite talus and rocks
	Leucopoa kingii	*Apocynum androsaemifolium*		Sparse vegetation
	Eriogonum umbellatum	*Epilobium canum*		
	Penstemon leonardii	*Solidago multiradiata*		
	Potentilla glandulosa	*Arenaria congesta*		
30		*Monardella odoratissima*	Ivgo/Mood	Subalpine talus and rocks
		Eriogonum caespitosum		Shallow soils
		Penstemon humilis		
		Artemisia dracunculus		
		Heuchera parvifolia		
31	*Artemisia tridentata*	*Comandra umbellata*	Artr/Coum	Low elevation dry rocky slopes
	Symphoricarpos oreophilus	*Balsamorhiza sagittata*		
		Elymus spicatus		

Unit	Alliance	Association	Label	Habitat
32	*Salix boothii*	*Salix wolfii*	Sabo/Sawo	High elevation wetlands
	Salix drummondiana	*Polygonum bistortoides*		
	Carex rostrata	*Pedicularis groenlandica*		
	Carex nebrascensis	*Juncus ensifolius*		
	Juncus balticus	*Saxifraga odontoloma*		
33		*Betula occidentalis*	Sabo/Beoc	Low elevation riparian
		Salix lutea		
		Salix lasiandra		
		Salix exigua		
		Cornus sericea		
34		*Ranunculus macounii*	Sabo/Rama	High elevation riparian
		Equisetum arvense		
		Arnica chamissonis		
		Geum macrophyllum		
		Veratrum californicum		

* Introduced species

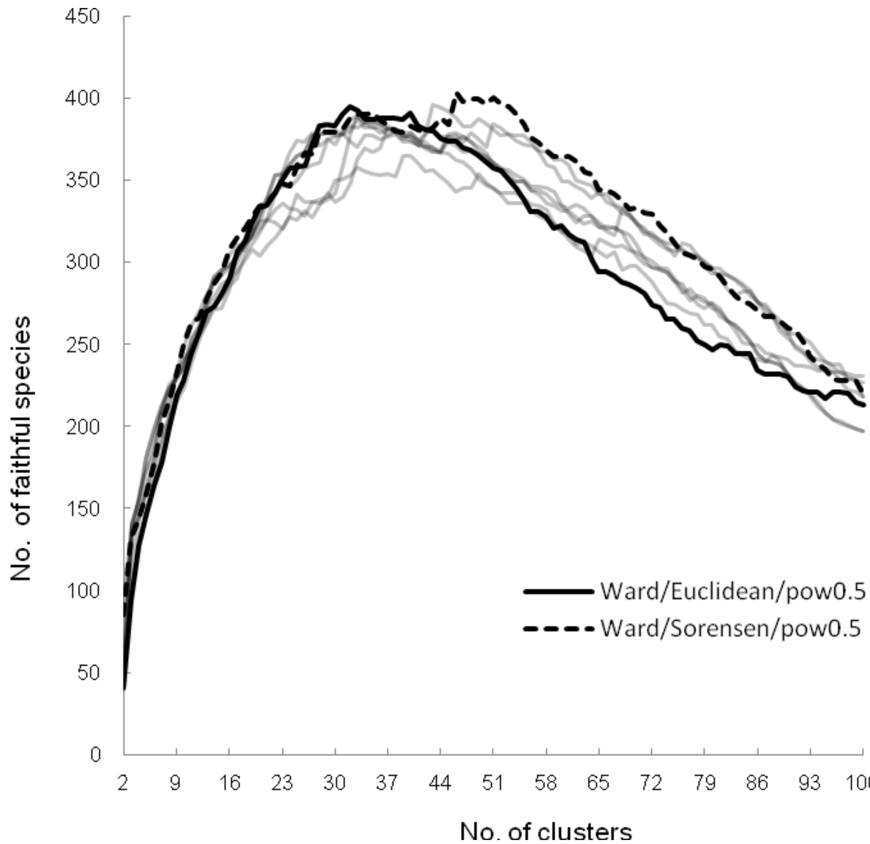

Figure 4.1. Results of the OptimClass method, Fisher's exact test with $p < 0.01$. Each of nine curves represents one solution based on partitioning method, distance measure and species cover transformation for number of clusters/vegetation units from 2 to 100 (on the horizontal axis). The vertical axis represents the total number of faithful species in all clusters for the given partitioning. Both bold and dashed curves are two best solutions in terms of the highest number of faithful species. The dashed curve represents statistically the best (403 faithful species in 48 clusters) but worst interpretable solution. The bold curve represents the most feasible solution with the highest number of faithful species (395) in 32 relatively large and interpretable clusters before final partitioning.

CHAPTER 5

COMPREHENSIVE ECOSYSTEM CLASSIFICATION IN THE ROCKY MOUNTAINS, NORTHERN UTAH [4]

Abstract

Fundamentals of the direct gradient analysis, hierarchical organization of terrestrial ecosystems together with the biogeoclimatic classification approach used in British Columbia were used to develop a comprehensive ecosystem classification in a mountainous study area in the northern Utah.

This classification was derived from sampling of both forest (spruce-fir, Douglas-fir, aspen, juniper and mahogany woodland) and non-forested (willow-riparian, shrublands, tall-forb meadows) ecosystems. One-hundred-sixty-three sample plots were described by physiographic features and soil properties such as nutrient pools and dynamics.

Principal component analysis revealed dominant environmental gradients affecting vegetation in the subalpine vegetation geo-climatic zone. We discriminated sample plots using cluster analysis, CART and RandomForests classification for each gradient, thus constructing an ecological grid and specifying site classes as the basis for the site classification. We coupled this site classification with existing vegetation classification, and allocated plant communities into an environmental space represented by the site grid. Within a broad climatic framework represented by the subalpine vegetation geo-climatic zone, this overlay resulted in a comprehensive ecosystem classification, allowing us to discriminate ecosystems.

[4] Coauthored by Antonin Kusbach, James N. Long, and Helga Van Miegroet

This classification enables a direct assessment of ecosystems' environmental properties and vegetation potential; and may allow us to infer site disturbance history and successional status of vegetation.

Introduction

"Show me your classification system, and I will tell you how far you are in elaborating the problem" - W. Kubiena

Early land classifications in the U.S., e.g., the habitat type concept (Daubenmire 1952), potential natural vegetation (Küchler 1969), and ecoregion classification (Bailey 1998), have been based on vegetation and macroclimate (Major 1951). Whereas habitat types rely completely on vegetation (Pfister 1976), other approaches for classifying terrestrial ecosystems, such as ecoregions, potential natural vegetation groups or biogeoclimatic zones (Krajina 1965), use combinations of vegetation and macroclimate based on the concept that broad macroclimate is reflected by similar vegetation over vast areas. However, vegetation is not driven only by macroclimate.

Following disturbances, ecosystems display a mosaic of plant communities in different successional stages. Together with animals, microbes and physical environment (hereafter referred to as a site), vegetation is a component of ecosystems irrespective of their size (Fosberg 1967, Pojar et al. 1987, Jennings et al. 2008). Thus, vegetation reflects the physical environment, disturbance history and biotic interactions (e.g., myccorhizae and allelopathy) and is dynamic. In contrast, the physical environment represents a relatively stable framework. Therefore, **comprehensive ecosystem classification** should include both vegetation and physical environment components.

Our general goal is to better understand the relationship between vegetation and physical environment in the study area representing the Rocky Mountains of northern Utah. To create a comprehensive ecosystem classification, we set out to: (1) construct a **site classification**, which organizes ecosystems, independent of vegetation strictly based on environmental properties; (2) couple this site classification with a **vegetation classification** which organizes plants according to their fidelity to a particular location (Chapter 4) to create a comprehensive ecosystem classification within the context of a broad climatic zonation or **zonal (climatic) classification** (Meidinger and Pojar 1991, Chapter 3).

Methods

Study area

Franklin Basin and the T.W. Daniel Experimental Forest make up the study area (ca 16,000 ha, and ca 1,000 m of vertical extent) (Fig. 2.2). Franklin Basin (FB, 15,000 ha) is a montane-subalpine area situated between the Bear River Range and the Wasatch Range in the central Rocky Mountains on the Utah and Idaho border. The T.W. Daniel Experimental Forest (TWDEF, ca 1000 ha) is situated on a high ridge plateau of the Wasatch Range (10 km to the southeast of FB).

According to Bailey (1998) and McNab et al. (2007), the study area occurs within M331 Southern Rocky Mountains Steppe-Open Woodland-Coniferous Forest-Alpine Meadow Province, “D” Overthrust Mountain Section, “n” Northern Wasatch Range, and “o” Bear River Front Range Subsections. The mean annual precipitation ranges from about 720 to 1250 mm and mean annual air temperature ranges from 2.4 to 5.7 ^{o}C for

Temple Fork, Tony Grove Lake, Franklin Basin, and Utah State University (USU) Doc Daniel weather stations (http://www.wcc.nrcs.usda.gov/snow/).

The terrain is mountainous, rocky and steep with occasional flat to gently sloping high ridge-plateaus and benches. The elevation ranges from 1590-3060 m across the three study sites. The highest area of the Bear River Range was glaciated during the Pleistocene as manifested by glacial geomorphologic features like moraines, U-shaped valleys, erratics, and irregular glacial deposits (Atwood 1909, Young 1939, Degraff 1976). The study area is mostly built from calcareous sedimentary rocks (limestone, dolomite) with interlayered quartzite, and from Tertiary sediments consisting of grit, conglomerate, and siltstone of Wasatch Formation at the TWDEF site. The soils are formed in residuum, colluvium, alluvium, glacial till and outwash, and occur on diverse landforms such as cliffs, talus slope, moraines, karst valleys, mountain slopes, landslides, plains, valleys, depressions, ravines, and wetlands (Schoeneberger et al. 2002).

Over half of the study area is occupied by forest ecosystems including Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), and woodland ecosystems including mountain mahogany (*Cercocarpus ledifolius*) and Rocky Mountain juniper (*Juniperus scopulorum*). Substantial changes in fire regimes, often in combination with cutting and grazing, have led to dramatic changes in the structure and the age-class distribution of forest stands. In many places, 100- to 140-year-old stands are now predominant (Long 1994). Forests in the study area are thus characterized by mid- and late-seral stages where forest understory is usually well developed (Pfister and Arno 1980). Non-forested ecosystems include willow-riparian habitats (*Salix spp.*) and wetlands, low shrublands

(*Artemisia spp.*), tall-forb meadows, and sparse vegetation on talus and rock outcrops, which may represent stable or temporary communities. Despite human impacts in last 120 years, the study area is considered as relatively natural in terms of plant species composition (Bird 1964).

Data collection

Sampling was intensive enough to capture as much ecosystem variation as possible focusing on all major existing plant communities (Brohman and Bryant 2005) occupying all major landforms (Schoeneberger et al. 2002), but avoiding ecotones and recently disturbed (burned, logged, damaged by insects) areas. For a site classification, we selected 136 sample plots within the subalpine zone (Chapter 3) from the entire dataset of 163 plots established in the summers of 2006 and 2007 in the study area (Chapter 2). A stratified (based on vegetation physiognomy) fixed (subjective selection) sampling design was used with circular plot size of 1000 m^2 for forest and 100 m^2 for non-forested ecosystems (Brohman and Bryant 2005). Three replicate plots were considered the minimum for defining a vegetation unit. We anticipated 50-60 units based on a preliminary reconnaissance of the study area.

We described each sample plot by environmental variables such as relatively static or constant attributes i.e., physiographic variables (slope aspect, slope gradient, topographic position and slope shape (Lotspeich 1980); dynamic attributes such as O and A horizon thickness, humus form, pH, nutrient pools, attributes describing relatively slow processes; and attributes such as nutrient supply rates describing relatively fast processes (Table 2.1). One soil pit was dug in each plot to the unweathered parent material and described using the National Cooperative Soil Survey protocols (Soil Survey Staff 1999, 2006, Schoeneberger et al. 2002). Humus form was identified following Green et al. (1993).

More detailed description of the various site characterization methods was provided in Chapter 2. Briefly, one composite soil sample from 0-30 cm was collected from a pedon face in each plot, air dried and sieved (< 2 mm), and the fine fraction analyzed for texture classes (sandy, loamy, clayey) using the feel-method (Thien 1979). Samples were then analyzed for pH (1:1 soil in water, Corning pH analyzer) and total C and N (LECO CN analyzer, Leco Corp., St. Joseph, MI). Exchangeable cations using a mechanical vacuum extractor (Holmgren et al. 1977), followed by extractant analysis on inductively-coupled plasma spectrophotometer (ICP) (Iris Advantage, Thermo Electron, Madison, WI); extractable P [the Olsen P method (Olsen et al. 1954), sodium bicarbonate extraction, Thermo Electron Spectronic 20 Genesys spectrophotometer]; and mineralizable N [7-day anaerobic incubation and extraction (Keeney and Bremmer 1966), NH_4 analysis (Lachat Quickchem 8000 Flow Injection Analyzer)] were determined as a static-absolute nutrient availability index (SNAI).

To determine a dynamic-relative nutrient availability index (DNAI) (Qian and Schoenau 2002), plant root simulators (PRS™-probes; Western Ag Innovations, Inc., Saskatoon, Canada), a combination of anion and cation exchange membranes, were buried vertically into the mineral soil at each site for six weeks (during September and November). PRS™-probes were cleaned and sent to Western Ag Innovations for extraction and chemical analysis including Ca, Mg, K, S, Fe, Mn, Zn, Cu, Pb, Al, NH_4 cations, and NO_3 and PO_4 anions (Table 2.1).

Data analysis

The dataset represented 136 sample plots and 42 environmental variables. We performed several analytical steps in order to discriminate sites that distinguish plant communities and reveal vegetation-site relationships. These included: (1) direct gradient analysis represented by ordination of environmental data; (2) cluster analysis of the important environmental variables; (3) discriminant analysis represented by Classification and Regression Trees (CART) and RandomForests of these environmental variables; (4) regressions among soil properties; and (5) overlay site classification with the previous vegetation classification (Chapter 4).

We used Principal components analysis (PCA) ordination (Pearson 1901) to determine the relative importance of the environmental factors to each principal component (PC) and interpret PCs as environmental gradients associated with the sample plots. Orthogonal rotations and correlation type of a cross-products matrix were used to get independent, mutually uncorrelated PCs (Lattin et al. 2003). Significance of PCs was tested by a Monte Carlo randomization test (based on proportion-based p-values for each PC). In order to document the relationship of the variables with the PCs and interpret PCs, we calculated correlation coefficients (loadings) with each ordination axis, and the linear (parametric Pearson's r) and rank (nonparametric Kendall's *tau*) relationships between the ordination scores and the observed variables. Our use of r and *tau* is suggested to be, even in relatively small datasets, more conservative than p-values for the null hypothesis of no relationship between ordination scores and variables (McCune and Grace 2002). We set the threshold for r and *tau* > 0.35. For variables conversion and transformation see Chapter 2.

To group the sample plots according to the important environmental factors obtained in the PCA, we ran a hierarchical cluster analysis for the environmental gradients; we used Ward's linkage method with compatible Euclidean distance matrix. We transformed the variables with $|\text{skewness}| > 1$ to be close to multivariate normality and standardized the data by adjustment to standard deviate (z-scores). We checked the dataset for outliers given cutoff of 2.0 standard deviations from the grand mean (McCune and Mefford 2006). Cluster dendrograms were scaled by a distance objective function (Wishart 1969) and resulting height rescaled for information remaining. The decision as to how many clusters to keep was based on a compromise between minimizing the number of clusters and maximizing of information retained i.e., on cluster stability (McCune and Grace 2002, Lattin et al. 2003). The best meaningful solution was verified by pseudo F function (Calinski and Harabasz 1974).

The cluster analysis grouped the plots by important environmental factors. Despite the grouping, we still did not know in what way the clusters differed. In order to detect cluster differences, we performed CART classification (Breiman et al. 1984) using "tree" function, and RandomForests (Breiman 2001) classification using "RandomForest" function in the R software. The CART classification was validated by 10-fold cross-validation and a classification tree was pruned to avoid over-fitting; this means we pruned the tree at a point where its additional growth did not bring any improvement. RandomForests classification verified the CART results. These two classifications highlighted: (1) the most important environmental factors associated with sites clustering along each gradient; and (2) possible misclassifications of sites. In addition, the CART classification provided factor's split thresholds that were used for labeling of relative **site**

classes. Based on this site classification, we constructed a **site grid** similar to an edatopic grid (Pogrebnyak 1930, Rysin 1982) for the subalpine vegetation geo-climatic zone.

We performed simple regressions of important nutrient concentrations and supply rates (N, P, K, Ca, Mg, Fe) with important soil properties suggested by the CART and RandomForests classification.

We overlaid the site classification represented by site classes in the site grid and the vegetation classification (Chapter 4) represented by plant associations within the subalpine zone (Chapter 3) to detect the relationship between environmental properties and existing vegetation. Each plant association was represented by minimum of three sample plots.

We used R software, ver. 2. 7. 2., (http://www.r-project.org/), and PC-ORD 5 (McCune and Mefford 2006) in the analysis.

Results

Environmental ordination

Principal component analysis (PCA) on the environmental data revealed four ecologically meaningful principal components (PC 1-4) (Table 5.1) that were interpreted as a soil nutrition, topography-moisture, microbial activity and soil development based on loadings (Table 5.2), and synthesized as soil fertility (PC 1, 3, 4), and topography-moisture (PC 2) gradients (Chapter 2). Based on PCs loadings, we identified eighteen important nutrient factors associated with a soil fertility gradient e.g., soil pH, $CaCO_3$ content, and nutrient SNAIs and DNAIs; and seven important topography factors representing a topography-moisture gradient such as slope position, slope gradient, terrain shape, soil depth, coarse rock fragment content, water table and mottles (Table 5.2). PCs were interpreted and synthesized in the same way as in the Chapter 2. Loadings were somewhat different from those reported in Table 2.3 because in current analysis only data set for the subalpine vegetation geo-climatic zone was used.

Cluster analysis

The important environmental indicators for soil fertility and topography-moisture gradient were used in cluster analysis to identify environmentally similar sites and assemble them into homogeneous clusters. This means that members of a cluster have similar soil fertility or topography-moisture properties but differ significantly from members of other clusters in those environmental parameters. Three-cluster and two-cluster solutions were statistically best for the topography-moisture and the fertility gradient, respectively, as indicated by amount information remaining and Pseudo F function. However, for meaningful ecological interpretation, the two-cluster solution of the fertility gradient was too general; therefore, we considered a similar three-cluster solution with broader interpretability also for the fertility gradient (Fig. 5.1a, b).

Discriminant analysis

Three-cluster solutions for both gradients were analyzed by CART and RandomForests. For the soil fertility gradient, CART performed a pruned classification tree with three terminal nodes based on splits of Al concentration and $CaCO_3$ content (Fig. 5.2a). Because $CaCO_3$ content represents soil alkalinity and Al concentration soil acidity, the terminal node 1 (Al_s $\geq$ 2.985 mg/kg soil) represents acidic sites, the terminal node 3 ($CaCO_3 \geq 0.35$ %) represents calcareous sites, and the terminal node 2 ($CaCO_3$ <

0.35 %; Al_s < 2.985 mg/kg soil) represents neutral or alkaline sites. The misclassification error rate was 7.4 % in the CART. RandomForests identified Al concentration and $CaCO_3$ content as environmental variables most strongly associated with the three-cluster solution of the fertility gradient (the first two variables in Fig. 5.2b). RandomForests was run with the number of trees (ntree) = 1000 and four variables used in each split (mtry = 4). Misclassification error rate was 6.6 %. CART and RandomForests results were consistent. Based on soil pH (the fourth variable in Fig. 5.2b) in combination with Al and $CaCO_3$ as additional parameters, the fertility gradient was expressed by three classes: (1) acidic; (2) neutral-alkaline; and (3) calcareous (Table 5.3a).

For the topography-moisture gradient, CART performed a pruned classification tree with three terminal nodes based on splits of soil depth and water table (Fig. 5.3a). The terminal node 1 (soil depth < 72.5 cm) represents sites with shallow soil, the terminal node 2 (soil depth > 72.5 cm; water table class > 3.5) represents sites with deep soils and no water table, and the terminal node 3 (soil depth > 72.5 cm; water table class < 3.5) represents sites with deep soils and water table present. CART calculated the misclassification error rate of 4.4 %. RandomForests calculated soil depth and water table as the variables most strongly associated with the three-cluster solution of the of the topography-moisture gradient (Fig. 5.3b). RandomForests was run with the number of trees (ntree) = 1000 and two variables used in each split (mtry = 2). Misclassification error rate was 1.5 %. CART and RandomForests results were consistent.

Three terminal nodes in this classification discriminated three topography-moisture classes, which were interpreted as: (1) convex/dry; (2) linear-concave/mesic; and (3) concave/wet (Table 5.3b). However, three-cluster classification for the topography-moisture gradient was too general and not sufficient to characterize the broad environmental variability of the gradient e.g., in the wet class, height of a water table is a fundamental driver of vegetation distribution. Therefore, each of those three clusters representing three preliminary topography-moisture classes were clustered and analyzed separately by CART and RandomForests to get more detailed structuring for the topography-moisture gradient.

In a repeated clustering (using the same Ward/Euclidean method), we assessed three-cluster solution as the best for the convex/dry and the concave/wet class, and two-cluster solution for the liner-concave/mesic class as the best as indicated by amount information remaining and Pseudo F function (Fig. 5.4a, b, c). In all instances, CART and RandomForests yielded consistent results. For the convex/dry class, CART performed a pruned classification tree with three terminal nodes based on coarse rock fragment content (RF) and slope gradient. The terminal node 1 (RF > 72.5 %; slope < 51.5 %) represents rocky, skeletal sites on backslopes, the terminal node 2 (RF > 72.5 %; slope > 51.5 %) represents steep rocky sites and cliffs, and the terminal node 3 (RF < 72.5 %) represents skeletal crests, shoulders and backslopes (Fig. 5.5a). CART calculated the misclassification error rate of 10.6 %. RandomForests also identified slope gradient and rock fragment content as the variables most strongly associated with the three-cluster solution of the convex/dry class (Fig. 5.5a). RandomForests was run with the number of trees (ntree) = 1000 and two variables used in each split (mtry = 2). Misclassification error rate was 6.1 %.

For the concave/wet class, CART performed a pruned classification tree with three terminal nodes based on slope position (topos) and water table. The terminal node 1 (topos > 3.5; water table > 60.5 cm) represents moist flats, the terminal node 2 (topos > 3.5; water table < 60.5 cm) represents wet flats and toeslopes, and the terminal node 3 (topos < 3.5) represents very wet concave footslopes (Fig. 5.5b). CART calculated the misclassification error rate of 6.3 %. RandomForests (ntree = 500, mtry = 2, error rate 6.3 %) also identified slope position and water table as most strongly associated with the two-cluster solution of the concave/wet class (Fig. 5.5b).

For the linear-concave/mesic class, CART performed a pruned classification tree with two terminal nodes based on variable mottles. The terminal node 1 (mottles > 3.5 meaning mottles are present) represents fresh, mostly concave toeslopes and depressions, and the terminal node 2 (mottles < 3.5 meaning no mottles) represents linear slopes (Fig. 5.5c). CART calculated the misclassification error rate of 2.1 %. RandomForests (ntree = 1000, mtry = 4, error rate 2.1 %) also identified mottles as most strongly associated with the two-cluster solution in this class (Fig. 5.5c).

As a result, the topography-moisture gradient was finally classified into eight classes: (1) extremely dry; (2) very dry; (3) dry; (4) slightly dry; (5) fresh; (6) moist; (7) wet; and (8) very wet (Table 5.3b).

Regressions of soil acidity and nutrient availability

Across the sampling plots, there was a significant negative association between soil pH and essential nutrient supply rates (N, P, K, Fe), i.e., at high pH, there were fewer nutrients available in a soil solution (Fig. 5.6). There was a significant positive correlation of Ca and Mg supply rates with soil pH, i.e., at high pH, there were enough Ca and Mg available in soil solution.

Regression results indicated lower plant nutrient supply of important macronutrients such as N, P, and K at high pH. This suggests that highly alkaline or calcareous soils are less fertile regardless of high supply of secondary macronutrients such as Ca and Mg.

Overlay of the site and vegetation classification

In a previous vegetation classification scheme, plant species were organized into plant alliances and associations (Table 5.4) (Chapter 4). Because each sample plot was associated with a specific site designation (based on topography-moisture and soil fertility) the plant associations could be organized into the site grid for the subalpine vegetation geo-climatic zone. This site-vegetation grid was constructed separately for forest (spruce-fir, Douglas-fir, mountain mahogany and aspen) and non-forested (sagebrush, tall-forb meadow and willow) ecosystems (Fig. 5.7). In this overlay, each plant association was characterized by **site quality**, a specific location in the grid identified by a particular combination of the soil fertility and topography-moisture within the environmental space. Once connected with site properties, these plant associations then represent an ecosystem, i.e., a relatively stable physical environment upon which the specific plant community grows (e.g., a riparian forest) (Major 1951, Pojar et al. 1987). Practically, we may recognize two or more different plant associations on a site with the same stable physical environment (these associations share a common space in the site grid). From this we may infer contrasting vegetation successional trajectories within the same relatively stable environmental context (D. Roberts 2009, personal communication).

Based on site quality, plant communities can be compared each other. While some associations are clearly detached from the others (e.g., 11, 12 mountain mahogany woodland in Table 5.4, Fig. 5.7b), others share the environmental space partially or entirely (e.g., 16-20 aspen in Table 5.4, Fig. 5.7d). This means that some communities (e.g., mountain mahogany on dry, calcareous, and rocky sites) occur in unique environmental settings, whereas others demonstrate a broad ecological amplitude (e.g., aspen).

Discussion

Site classes

A two-step consecutive differentiation within the topography-moisture gradient revealed eight meaningful topographical-moisture classes, while a simpler division did not explain ecosystem distribution along the gradient adequately. Local topography is a fundamental predictor of physical soil properties (especially soil depth, rock fragment content and slope gradient) that affect soil water status, including drainage (Schoeneberger et al. 2002).

Aridity of the classes 1 through 3 is reflected by high rock fragment content, high slope position, steep slope gradient and shallow soils. Soils within these classes remain dry for a long period of the year especially in summer. Mesic conditions of the classes 4 through 5 are expressed by greater soil depth and by the presence of mottles, which indicate water stagnation in a soil profile for some time during the year. These soils may remain moist for a substantial period of the year especially after spring runoff. Wetness of the classes 6 through 8 is expressed by depth to the water table fluctuating in a soil profile throughout a year. With a perched water table, soils of these classes remain wet for the entire year.

The wet classes (6 through 8) may be characterized by surplus of soil water throughout the year while the dry classes (1 through 3) experience substantial water deficits. The mesic classes (4 through 5) could be considered more or less balanced in terms of soil water supply depending on climatic inputs (amount of precipitation as a snowpack in winter wet season).

Soil pH emerged as the strongest indicator of the fertility gradient. It is strongly correlated with the plant nutrient availability (Fig. 5.6) (e.g., Lindsay 1976, Kotar 1988, Brady and Weil 1999). Relatively acid soils in class 1 are associated with presence of quartzite or its weathered remnants (rich in silica) especially in glacial deposits (till). Such soils with high amount of Al and H (acidic) cations, and little or no $CaCO_3$ are subject to greater leaching of important nutrients such as base cations (K, Ca, Mg) especially in a humid mountainous climate. This results in low plant nutrient availability and low soil fertility.

Because of the generally alkaline status of soils derived from alkaline limestone and dolomite rocks, soils in class 2 have high buffering capacity, i.e., high ability to resist pH change. Soil fertility is high as important base nutrients are retained on the soil exchange complex (high base saturation) and other macronutrients (N, P, and S) are relatively available (Brady and Weil 1999, Montana State University 2005).

In dry, calcareous environment of soils in class 3, all important macronutrients (primary macronutrients N, P, K) are less available for plants (Lindsay 1976, Brady and Weil 1999). The supply rates of NH_4, P, K and Fe are low at high pH (Fig. 5.6); K is fixed in minerals (mainly clays) in dry conditions; similarly Ca is precipitated as $CaCO_3$; and important micronutrients (metals) are fixed in minerals or bound tightly to the soil (Brady and Weil 1999, Montana State University 2005). As a consequence, calcareous sites can experience important nutrient deficiencies and appear to be less productive due to aridity, i.e., soil water is the strongest driver of plant nutrient availability (Lindsay 1976, Brady and Weil 1999, Montana State University 2005). Note that all cells for this calcareous class and classes 4-8 of the topography-moisture gradient are empty indicating that there are no moist or wet calcareous sites (Fig. 5.7).

Allocation of plant communities

The association of plant communities (associations) and environmental factors represented by the site-vegetation grids (Fig. 5.7) provides considerable insight into the influence of environmental gradients on the distribution of vegetation, likely successional patterns (ecosystem dynamics), and even particular misclassifications of plant communities that might have happened in vegetation classification (Chapter 4).

A great advantage of the site classification is that plant communities are mutually comparable inside the site grid. Sites with the same quality have the same vegetation potential (Cajander 1926, Bakuzis 1969), that is, are capable of supporting the same climax vegetation. The presence of different existing plant communities indicates that they likely experienced different succession or different disturbance history (e.g., Pojar et al. 1987, McCune and Grace 2002) (consistent with the concept of alternate states in rangeland e.g., NRCS Ecological Site Description, Ripplinger 2010). Thus, representation of plant communities within the site grid allows assessment of environmental-disturbance relationships and ecosystem dynamics (Pojar et al. 1987, Meidinger and Pojar 1991, D. Roberts 2009, personal communication).

In the site grid, some plant communities seem to be detached from the others while others share the environmental space partially or entirely. For example, the 12-Cele/Pepu mountain mahogany is the only community occurring on extremely dry calcareous sites (Fig. 5.7b). This unique environmental setting is thus a good predictor of mountain mahogany climax vegetation. In contrast, the 5-Abla-Pien/Lipo and 6-Abla-Pien/Osch spruce-fir communities (Table 5.4) share a similar space in the site grid (Fig. 5.7a). Similarly, the Douglas-fir 14-Psme-Abla-Pifl/Linu and 15-Psme-Pifl/Aste penetrate (Fig. 5.7c). Spruce-fir communities 5 and 6 were classified differently because of different age, yet were considered as one ecosystem (mild, undulating slope forest) growing in a similar environment (Table 5.4). In the case of Douglas-fir communities, different classes in an apparently similar environment may be explained either by different elevations of Douglas-fir communities which cannot be displayed in the site grid (the site grid is constructed for one vegetation geo-climatic zone only, Chapter 3) or by succession, i.e., on the basis of different age of the Douglas-fir stands. Here again, these communities were considered as one ecosystem (subalpine/high elevation sunny-slope forest) (Table 5.4).

Aspen communities cover a large space inside the grid reflecting its exceptional ecological plasticity and amplitude (e.g., Mueggler 1988, Klinka et al. 1999, Chapter 3) and high genetic variability (Mock et al. 2008). Aspen does not occur on very wet sites (class 8) or extremely dry sites (class 1). It is most prevalent in the center of the site grid (in intermediate environmental condition – topo-moisture class 3, 4 and fertility class 2) where four associations share the similar space (16-19 in Table 5.4, Fig. 5.7d). There is essentially low environmental difference among those communities that is consistent with their somewhat weak vegetation classification (Chapter 4). On the other hand, despite some similarity of relatively poor (16-Potr-Abla-Pien/Pole, blue color in Fig. 5.7d) and alkaline/calcareous (19-Potr-Abla/Scla; yellow) aspen with others, these two communities together with wet aspen (20-Potr/Cyof, orange) indicate that reasonable environmental difference among the extremes exists within aspen communities. These environmental extremes are more obvious from continuous ordination space based on PCA (Fig. 5.8) rather than from categorical classes of a site grid (Fig. 5.7d). The wet aspen community (20-Potr/Cyof) is the only true separate group (no common space with any of others) with clearly different environment that might be considered potential stable riparian broad-leaved forest ecosystem (Table 5.4). Conifer encroachment into aspen communities (16-19-Potr-abla associations) is indicative of successional transition. Based on the site grid, conifer encroachment does not seem to be associated with specific environmental site properties. Absence of conifers in moist and wet aspen community (20-Potr/Cyof) seems to indicate that this community may be more resistant to conifer encroachment than the others.

The display of plant communities within the site grid can also reveal potential mistakes in vegetation classification. For example, the 7-Abla-Pien-Psme/Rupa spruce-fir association occurs in two clearly detached places in the grid. Environmental difference of two site classes between these two places (from slightly dry to extremely dry) (Fig. 5.7a) is so large that they cannot be considered the same plant association. There is an obvious misclassification of the spruce-fir association (7); this association should be reclassified and divided into two separate communities.

For non-forested plant communities, there is a clear environmental difference between two major sagebrush communities: *Artemisia spiciformis* (Shultz 2009) (21, 22, 23) and *Artemisia tridentata* sub. *vaseyana* (31) (Fig. 5.7e). While the first occurs on more mesic sites, the second occurs on dry and alkaline-to-calcareous conditions. *Artemisia spiciformis* associations penetrate each other and also share a similar space with spruce-fir and aspen forest communities. This indicates either potential successional transition of the sagebrush communities towards conifer/aspen forest or local climatic differences such as cold air drainage in valley bottoms between relatively stable sagebrush communities and surrounding forest ecosystem (Table 5.4). This cold air drainage, where 21 and 22 - *Artemisia spiciformis* occur, may maintain sagebrush stability by preventing of forest establishment. The 31 - *Artemisia tridentata* association shares a similar environmental space with juniper and mountain mahogany associations suggesting transitional possibilities of sagebrush steppe towards these woodland types (Fig. 5.7b, e).

Potential value of a comprehensive classification

The comprehensive ecosystem classification resulting from the joining of the site and vegetation classifications demonstrated a considerable influence of the physical environment (climate and site) on vegetation distribution. The allocation of plant communities inside the site grid appears to be a powerful tool for ecosystem environmental assessment. Because vegetation distribution is influenced not only by environmental factors (site properties), but also by disturbance history, knowledge of vegetation environmental demands can help us to infer vegetation dynamics and succession.

The comprehensive ecosystem classification as demonstrated for the subalpine vegetation geo-climatic zone (Chapter 3) may be used as a means of communication in ecosystem research, outreach and education, as well as a tool for practical interpretations and applications in ecosystem management (Pojar et al. 1987, Kotar 1988, Sharik 2010). For example, based on a particular climate change scenario and knowledge of current site quality of ecosystems we can infer potential change in site properties (e.g., soil chemistry microclimate), from which we can predict possible ecosystem changes and transition. Additionally, knowledge about the site quality may contribute to ecosystem planning, conservation or utilization.

Summary and conclusions

Our site classification was based on the most important environmental factors and gradients within the subalpine vegetation geo-climatic zone. These gradients were topography-moisture and fertility. We specified important site classes associated with each gradient and constructed a site grid. We overlaid the existing vegetation classification onto the site classification, resulting in allocation of plant associations into the site grid. This comprehensive classification integrated zonal classification with both vegetation and environmental classification and enabled environmental specification of existing vegetation. Each plant community was defined by a particular site quality and compared with other communities within the framework of the site grid (an environmental space of the subalpine vegetation geo-climatic zone).

This specification and comparison is important in understanding the relationship of vegetation with physical environment in the study area. Based on vegetation comparison, we were able to identify distinct ecosystems and infer possible ecosystem dynamics i.e., we could ascertain site disturbance history and successional status of vegetation.

Compared to the Natural Resources Conservation Service (NRCS) Ecological Site Description (ESD), which is soil-based and works largely for low-elevation rangelands, our classification assesses a broader range of important ecosystem components; it reflects relationships between climate, vegetation and physical site factors across a range of both forest and non-forested ecosystems. Our classification included all potential ecosystems in the study area; we assessed conifer and broad-leaved woodland, conifer and broad-leaved forest as well as non-forested ecosystems such as riparian wetland shrubland, dwarf-shrubland sagebrush steppe, tall-forb subalpine meadows, and sparse vegetation of highest mountain peaks.

The comprehensive ecosystem classification should serve as a general means of communication and therefore may be used as a valuable tool not only in ecosystem research but also in practical ecosystem management.

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Table 5.1. PCA summary with interpretation and synthesis of principal components. Significant principal components are indicated by *p* values, ecologically meaningful-interpretable PCs are in bold. NA-not applicable.

	PC1	**PC2**	**PC3**	**PC4**	PC5	PC6
Eigenvalue	**8.34**	**7.41**	**4.99**	**2.54**	2.21	1.59
% of Variance	**19.85**	**17.66**	**11.89**	**6.04**	5.26	3.78
Cumulative % of Var.	**19.85**	**37.49**	**49.38**	**55.41**	60.67	64.44
p- value	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0002	0.99
Interpretation	Soil nutrition	Topo-moisture	Microb. activity	Soil development	NA	NA
Synthesis	**Soil fertility**	**Topo-moisture**	**Soil fertility**		NA	NA

Table 5.2. PCA loadings. Significant Pearson's (r), and Kendall's (tau) coefficients are in bold; both significant loadings express a significant variable for the particular PC (shaded). Variables are defined in Table 2.1.

PC	PC1		PC2		PC3		PC4
Variable	r	tau	r	tau	r	tau	r
topos	-0.15	-0.14	**-0.81**	**-0.65**	0.11	0.00	-0.01
sl	0.14	0.16	**0.64**	**0.49**	0.16	0.09	-0.01
av	-0.31	-0.23	-0.05	-0.05	**0.37**	0.25	0.00
shape	-0.16	-0.11	**-0.72**	**-0.63**	-0.08	-0.07	0.16
Ohor	0.02	0.01	**-0.37**	-0.25	**0.76**	**0.43**	0.06
Ahor	0.11	0.11	-0.27	-0.21	**-0.62**	**-0.47**	0.10
hum	0.06	0.03	0.29	0.21	**-0.72**	**-0.45**	-0.09
sdepth	-0.32	-0.20	**-0.70**	**-0.55**	-0.10	-0.08	0.18
RF	0.07	0.06	**0.70**	**0.56**	0.17	0.11	-0.24
parmat	0.43	0.28	**-0.56**	**-0.40**	-0.25	-0.19	0.14
wtable	-0.10	-0.07	**0.68**	**0.45**	**-0.35**	-0.23	0.19
mottles	-0.04	-0.03	**0.74**	**0.52**	-0.32	-0.20	0.12
cvalue	**-0.74**	**-0.60**	0.24	0.08	0.09	0.12	0.03
text	**0.41**	0.31	**-0.48**	-0.28	0.17	0.07	0.05
pH	**0.85**	**0.66**	0.23	0.16	-0.06	-0.04	0.05
CaCO3	**0.73**	**0.59**	**0.42**	**0.38**	0.11	0.10	0.02
Nmin_d	0.09	0.06	0.17	0.12	**-0.65**	**-0.48**	-0.34
Nox	**0.60**	**0.43**	**-0.41**	-0.23	-0.15	-0.25	-0.07
NO3_d	0.10	0.07	0.17	0.12	**-0.68**	**-0.52**	-0.31
NH4_d	-0.24	-0.14	-0.01	0.03	**0.43**	0.31	-0.15
Cox	**0.76**	**0.62**	-0.23	-0.04	0.10	-0.02	-0.03
C/N	0.31	0.17	0.29	0.20	**0.47**	**0.38**	0.07
Ca_d	**0.48**	0.32	-0.26	-0.16	**-0.36**	-0.24	-0.04
Mg_d	**0.59**	**0.38**	-0.02	-0.02	0.17	0.08	-0.13
K_d	**-0.62**	**-0.43**	0.07	-0.08	**-0.41**	-0.24	0.14
P_d	**-0.38**	-0.28	-0.28	-0.25	**-0.49**	-0.34	0.11
Fe_d	-0.33	-0.24	**-0.60**	**-0.36**	-0.05	-0.10	-0.31
Mn_d	**-0.48**	**-0.37**	**-0.35**	-0.20	0.18	0.07	-0.27
Zn_d	-0.07	-0.04	**-0.36**	-0.18	**-0.44**	-0.31	-0.29
S_d	-0.29	-0.23	**-0.43**	-0.21	0.16	0.06	-0.34
Al_d	-0.07	-0.04	0.19	0.12	-0.21	-0.13	-0.14
Ca_s	**0.80**	**0.62**	**-0.35**	-0.13	-0.03	-0.08	0.06

Mg_s	**0.83**	**0.65**	-0.17	-0.10	0.27	0.09	-0.01
K_s	0.07	0.05	**-0.35**	-0.28	**-0.44**	-0.31	0.25
NH4_s	0.07	0.01	**-0.56**	**-0.35**	0.10	0.02	-0.05
Nmin_s	**0.66**	**0.48**	**-0.49**	-0.22	0.00	-0.12	-0.09
P_s	-0.33	-0.22	-0.33	-0.29	**-0.45**	**-0.35**	0.11
Al_s	**-0.73**	**-0.59**	0.11	0.04	0.30	0.24	-0.03
Fe_s	**-0.35**	-0.28	-0.06	-0.05	**0.44**	**0.35**	-0.02
S_s	-0.02	0.04	**-0.55**	**-0.35**	-0.05	-0.03	-0.02
Mn_s	**-0.65**	**-0.49**	-0.34	-0.30	-0.12	-0.08	0.11
Zn_s	**-0.55**	**-0.41**	-0.02	-0.03	0.08	0.07	-0.03

Table 5.3. Site classification and site class specification: a) topography-moisture gradient; b) fertility gradient. Variables are defined in Table 2.1.

a

1 Acidic	2 Neutral-alkaline	3 Calcareous
pH 5.8 (5.7, 5.9)[a]	pH 6.5 (6.4, 6.6)[a]	pH 7.6 (7.5, 7.7)[a]
$CaCO_3$ = 0 %	$CaCO_3$ < 0.35 %	$CaCO_3 \geq$ 0.35 %
Al ≥ 2.985 mg/kg soil	Al < 2.985 mg/kg soil	Al = 0 mg/kg soil

[a] Mean (95 % confident limits), $F = 217.2$, $p < 0.0001$, $N = 136$

b

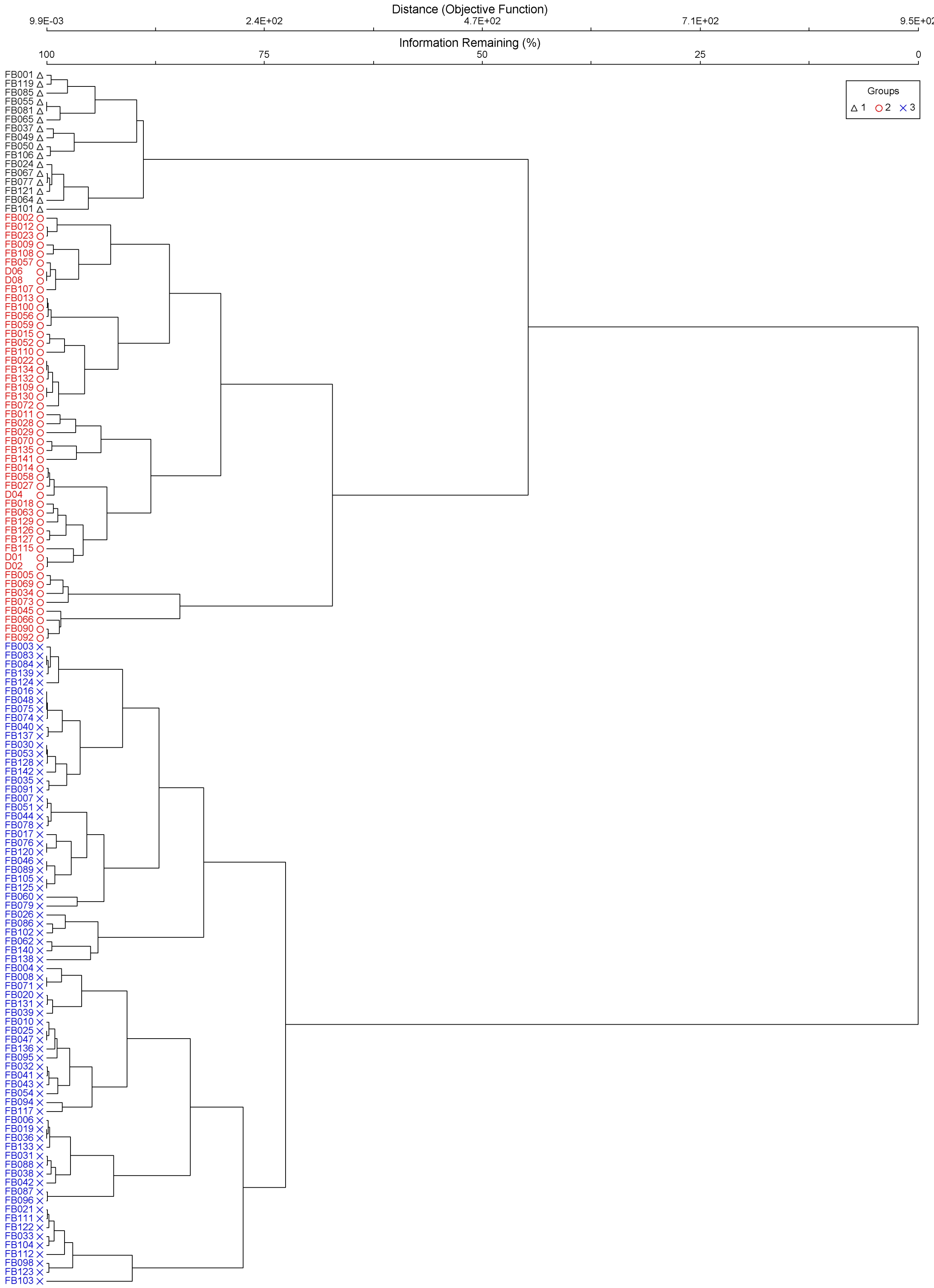
First run	**1 Convex/dry**			**3 Linear-concave/mesic**		**2 Concave/wet**		
Preliminary classes	Shallow soils < 72.5 cm NO water table Summits, shoulders, backslopes			Deep soils ≥72.5 cm NO water table Mottles may present > 30 cm Flats, back-, foot-, toeslopes		Deep soils ≥ 72.5 cm Water table present Mottles ≤ 30 cm Flats, toeslopes		
Repeated run	**1 Extr. dry**	**2 Very dry**	**3 Dry**	**4 Slightly dry**	**5 Fresh**	**6 Moist**	**7 Wet**	**8 Very wet**
	RF > 72.5 %	RF > 72.5 %	RF ≤ 72.5 %	NO mottles	Mottles present	Water table > 60.5 cm	Water table < 60.5 cm	Water table < 30 cm
	sl > 51.5 %	sl ≤ 51.5 %				Mottles ≤ 60 cm	Mottles ≤ 35 cm	
	sdepth < 40 cm	sdepth < 50 cm	sdepth < 70 cm	Linear	Concave	Linear	Linear -concave	Concave
	Steep slopes Cliffs	Backslopes	Crests Shoulders Backslopes	Backslopes Toeslopes Footslopes	Toeslopes Depressions	Flats	Flats Toeslopes	Footslopes

Table 5.4. Plant alliances and associations, and ecosystems.

No	Alliance	Association	Label	Ecosystem
1	*Abies lasiocarpa* *Picea engelmannii*	*Galium boreale*	Abla-Pien/Gabo	Riparian forest
2		*Zigadenus elegans*	Abla-Pien/Ziel	Wetland forest
3		*Thalictrum fendleri*	Abla-Pien/Thfe	High elevation, valley bottom open-canopy forest
4		*Lonicera utahensis*	Abla-Pien/Lout	Subalpine shady-slope forest
5	*Abies lasiocarpa* *Picea engelmannii* *Populus tremuloides*	*Ligusticum porteri*	Abla-Pien-Potr/Lipo	Mild, undulating slope forest
6		*Osmorhiza chilensis*	Abla-Pien-Potr/Osch	
7	*Abies lasiocarpa* *Picea engelmannii* *Pseudotsuga menziesii*	*Rubus parviflorus*	Abla-Pien-Psme/Rupa	High elevation skeletal shady-slope forest
8		*Rubus idaeus*	Abla-Pien-Psme/Ruid	Quartzite talus forest
10	*Juniperus scopulorum*	*Lomatium grayi*	Jusc/Logr	Very dry skeletal slope conifer woodland
11	*Cercocarpus ledifolius*	*Mertensia oblongifolia*	Cele/Meob	Dry slope broad-leaved woodland
12		*Petradoria pumila*	Cele/Pepu	Extremely dry, rocks/cliff broad-leaved woodland
13	*Pseudotsuga menziesii* *Abies lasiocarpa*	*Acer grandidentatum*	Psme-Abla/Acgr	Low elevation shady-slope forest

No	Alliance	Association	Label	Ecosystem
14	*Pseudotsuga menziesii* *Pinus flexilis* *Abies lasiocarpa*	*Linanthastrum nuttallii*	Psme-Abla-Pifl/Linu	Subalpine/high elevation sunny-slope forest (ribbons)
15	*Pseudotsuga menziesii* *Pinus flexilis*	*Astragalus tenellus*	Psme-Pifl/Aste	
16	*Populus tremuloides* *Abies lasiocarpa* *Picea engelmannii*	*Poa leptocoma*	Potr-Abla-Pien/Pole	Mild, undulating slope forest
17	*Populus tremuloides* *Abies lasiocarpa*	*Valeriana occidentalis*	Potr-Abla/Vaoc	
18		*Symphoricarpos oreophilus*	Potr-Abla/Syor	
19		*Scrophularia lanceolata*	Potr-Abla/Scla	Low elevation broad-leaved forest
20	*Populus tremuloides*	*Cynoglossum officinale*	Potr/Cyof	Riparian broad-leaved forest
21	*Artemisia spiciformis*	*Chrysothamnus viscidiflorus*	Arsp/Chvi	Low elevation valley bottom/slope dwarf-shrubland (sagebrush steppe)
22		*Poa arnowiae*	Arsp/Poar	High elevation valley bottom/slope dwarf-shrubland (sagebrush steppe)
23		*Agastache urticifolia*	Arsp/Agur	
25	*Rudbeckia occidentalis*	*Ranunculus adoneus*	Ruoc/Raad	Subalpine depression/colluvial outwash meadow
26	*Agastache urticifolia*	*Aster integrifolius*	Agur/Asin	Subalpine flat/mild slope meadow
28	*Linum kingii*	*Hymenoxys acaulis*	Liki/Hyac	Alpine talus and rock sparse vegetation meadow
29	*Ivesia gordonii*	*Juncus parryi*	Ivgo/Jupa	Quartzite talus and rock sparse vegetation meadow
30		*Monardella odoratissima*	Ivgo/Mood	Subalpine talus and rock sparse vegetation meadow
31	*Artemisia tridentata*	*Comandra umbellata*	Artr/Coum	Low elevation dry rocky slope dwarf-shrubland (sagebrush steppe)
32	*Salix boothii*	*Salix wolfii*	Sabo/Sawo	High elevation wetland shrubland
33		*Betula occidentalis*	Sabo/Beoc	Low elevation riparian shrubland
34		*Ranunculus macounii*	Sabo/Rama	High elevation riparian shrubland

a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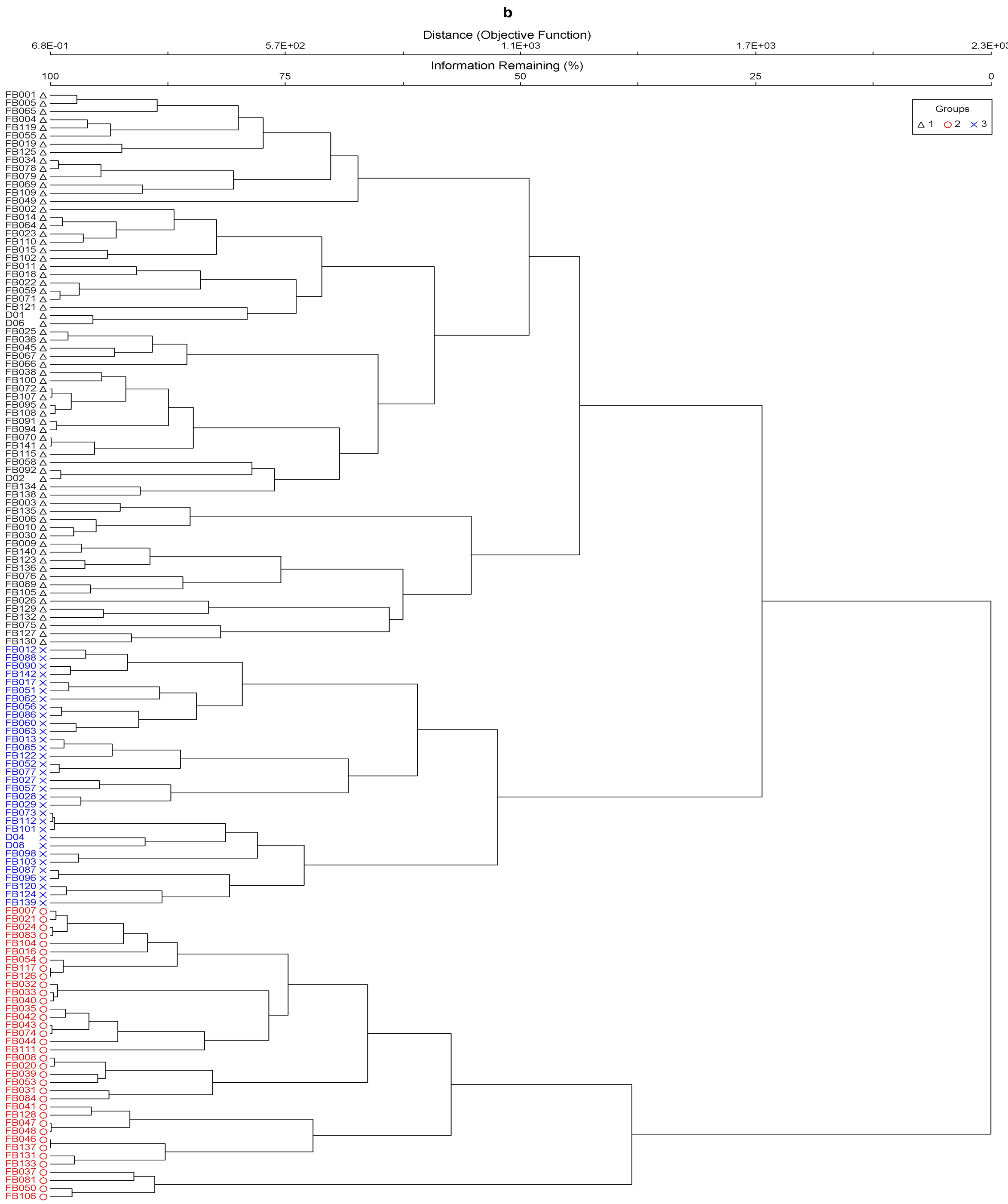


Figure 5.1. Cluster analysis of environmental gradients. Three cluster solutions for: a) topography-moisture gradient; b) fertility gradient. See text for explanation.

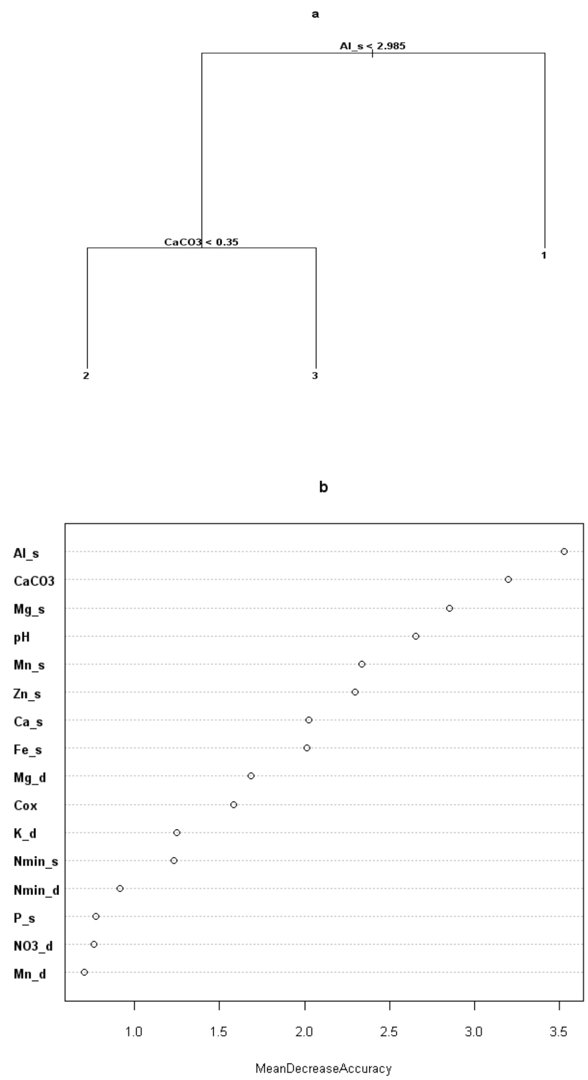


Figure 5.2. CART and RandomForests classification of the fertility gradient: a) a pruned classification tree with thresholds of important variables and three terminal nodes, each represents one fertility class; b) variable importance in RandomForests analysis. Variables are defined in Table 2.1. See text for explanation.

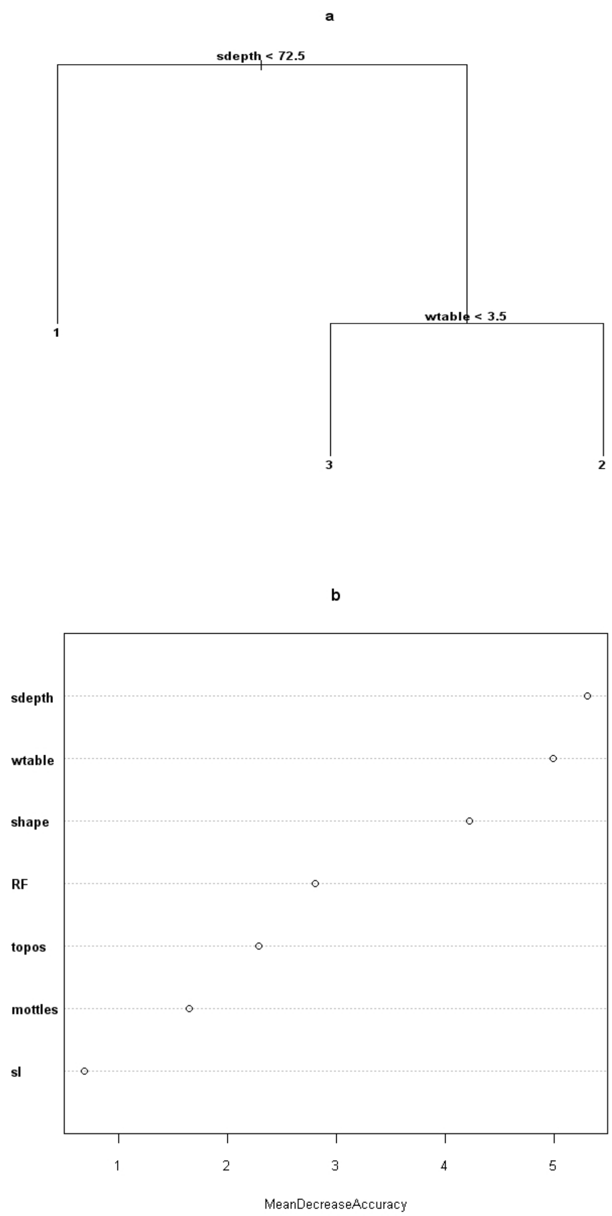
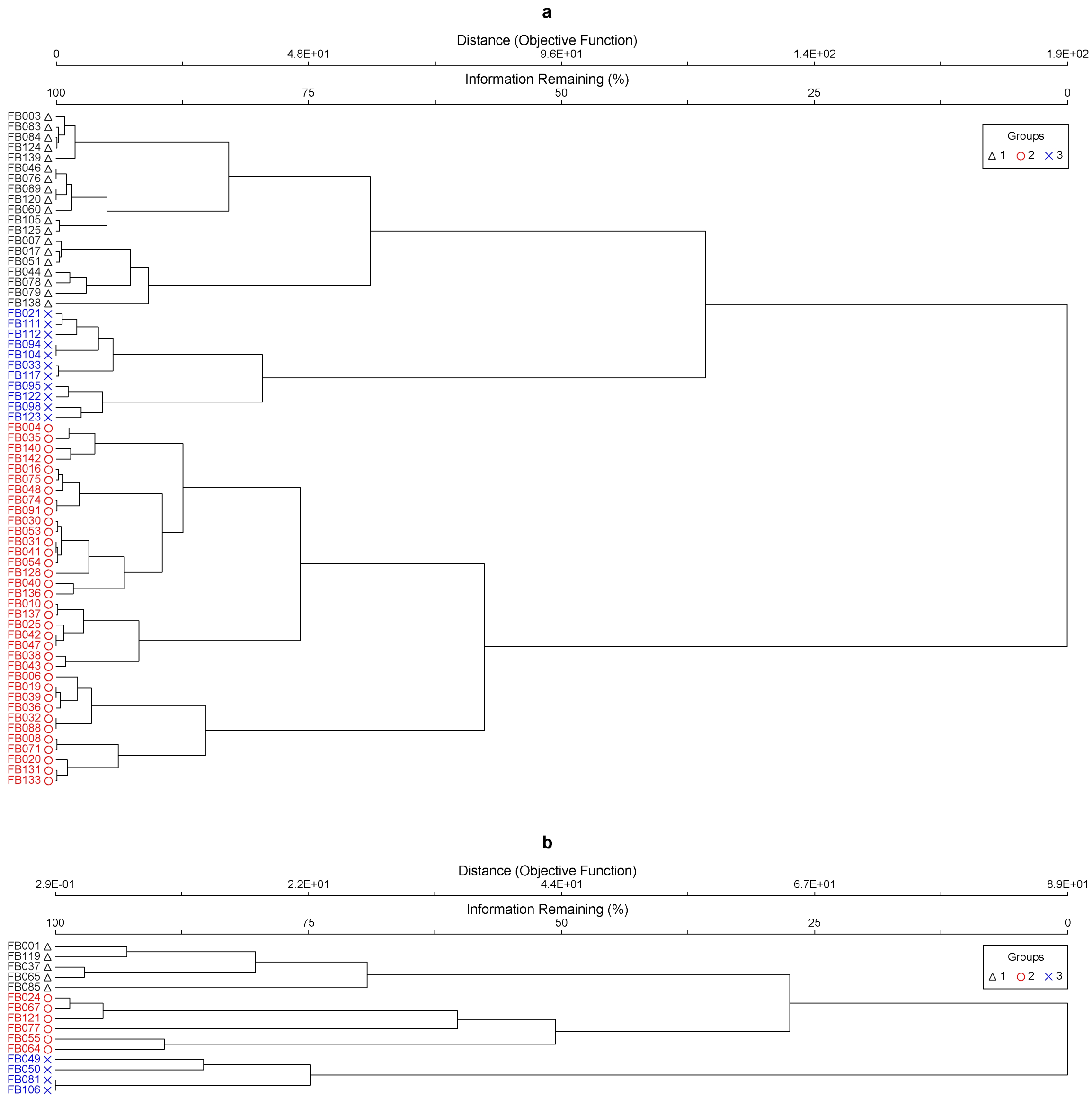


Figure 5.3. CART and RandomForests classification of the topography-moisture gradient: a) a pruned classification tree with thresholds of important variables and three terminal nodes, each represents one topography-moisture class; b) variable importance in RandomForests analysis. Variables are defined in Table 2.1. See text for explanation.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9.6E+01
1.4E+02
1.9E+02
Information Remaining (%)
100
75
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Groups
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2.2E+01
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6.7E+01
8.9E+01
Information Remaining (%)
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75
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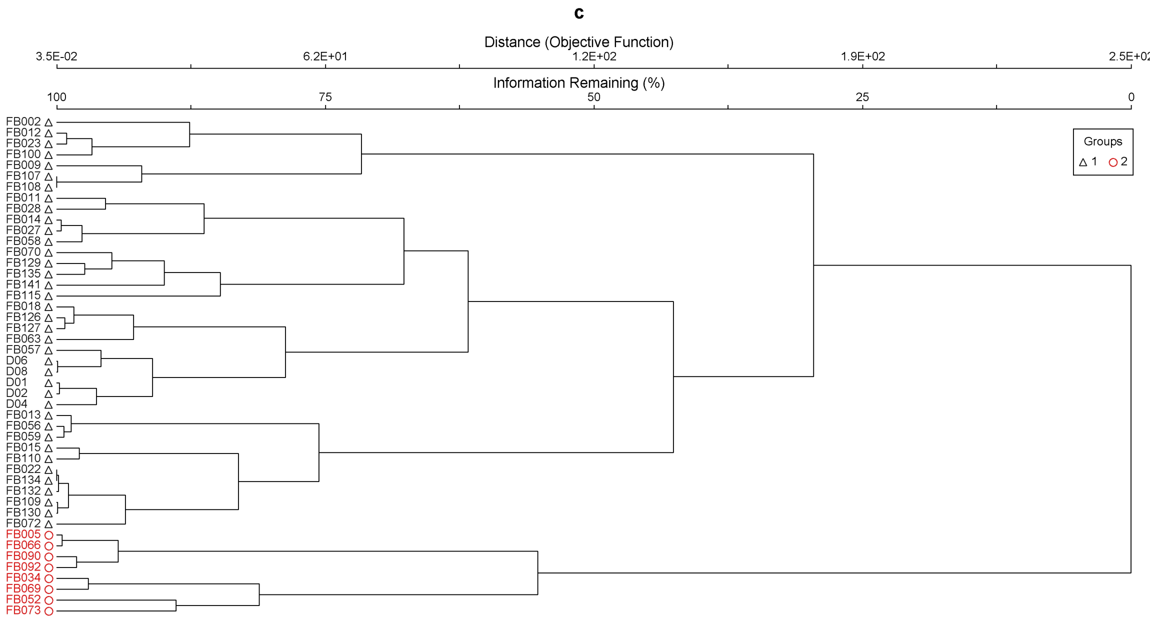
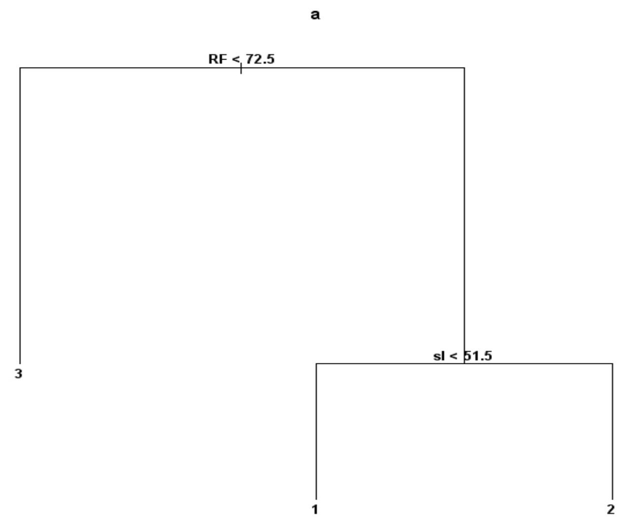


Figure 5.4. Cluster analysis of three topography-moisture classes: a) convex-dry; b) concave-wet; and c) linear-concave-mesic.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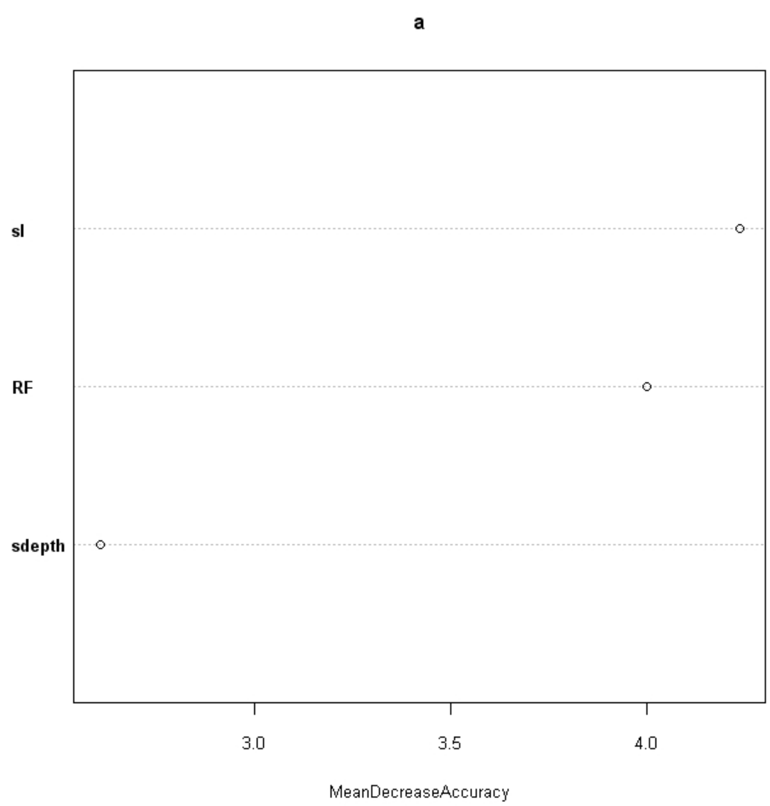
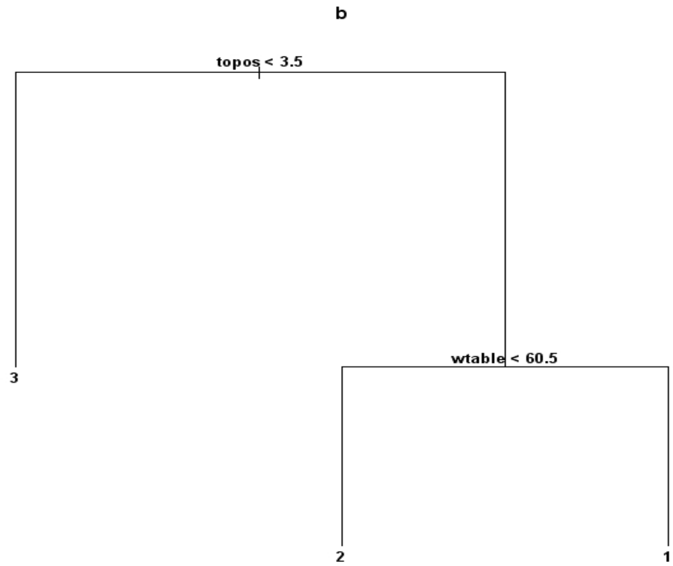
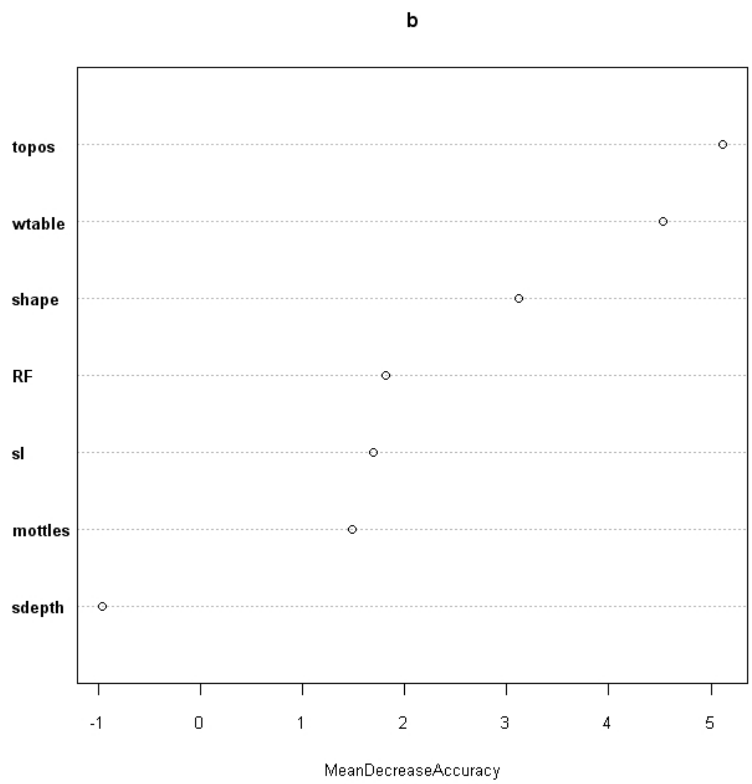
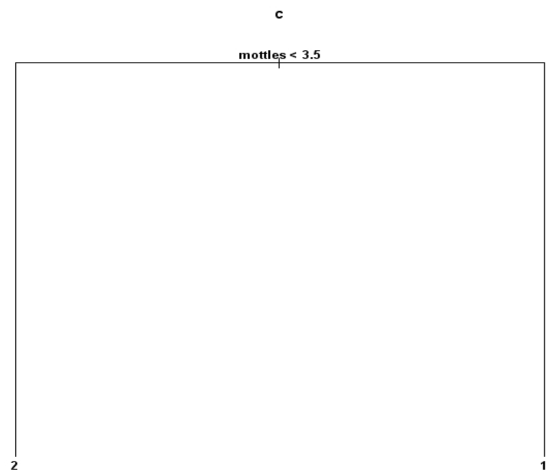
1
2


a
sl
RF
sdepth
3.0
3.5
4.0
MeanDecreaseAccuracy


b
topos < 3.5
wtable < 60.5
3
2
1


b
topos
wtable
shape
RF
sl
mottles
sdepth
-1
0
1
2
3
4
5
MeanDecreaseAccuracy



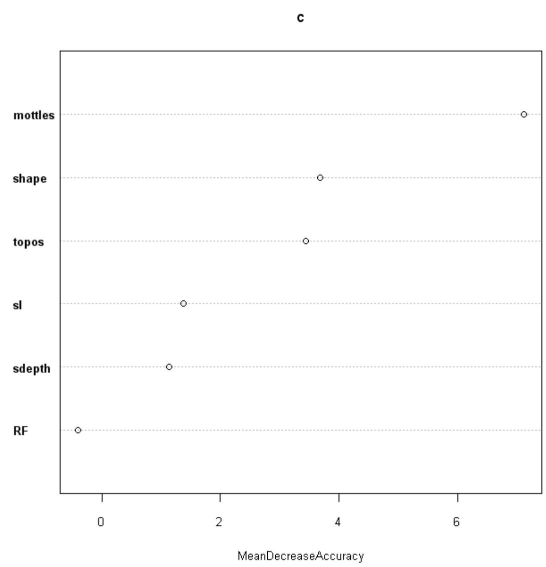


Figure 5.5. CART and RandomForests classification of the topography-moisture classes: a) convex-dry; b) concave-wet; and c) linear-concave-mesic. Pruned classification trees with thresholds of important variables and terminal nodes for final topography-moisture classes. Variable importance in RandomForests analysis. Variables are defined in Table 2.1. See text for explanation.

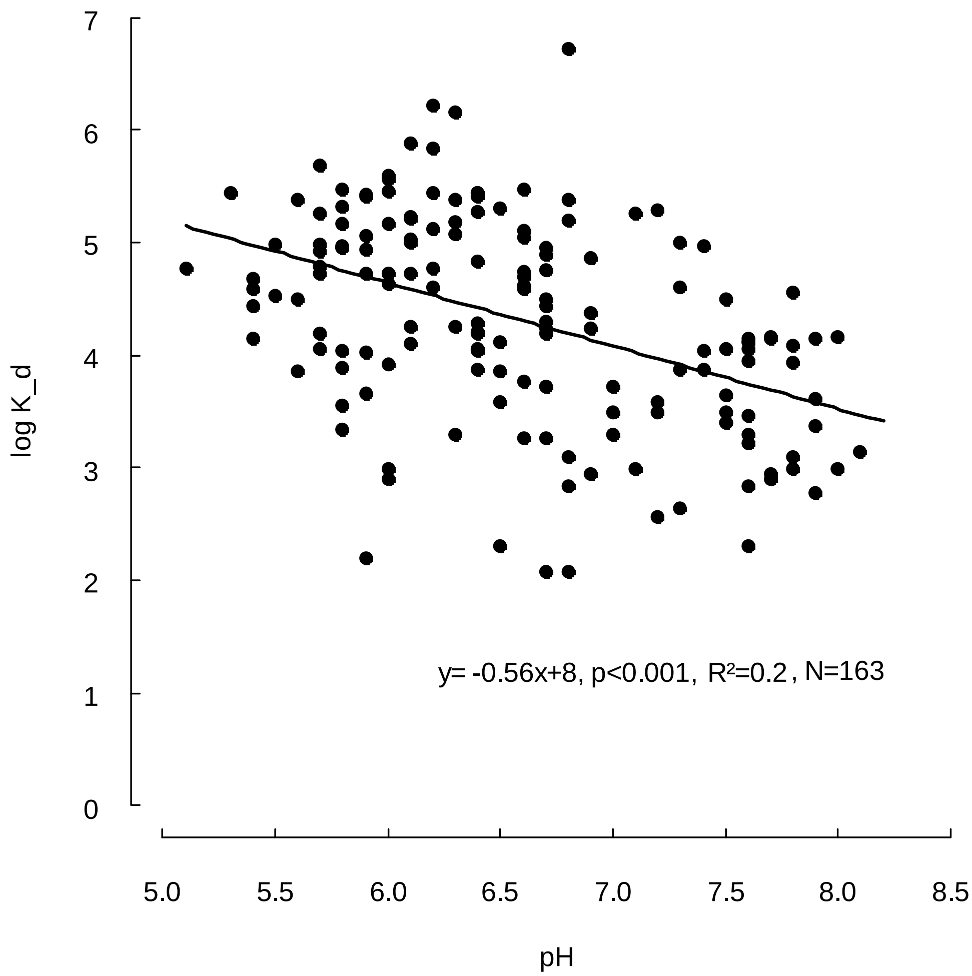
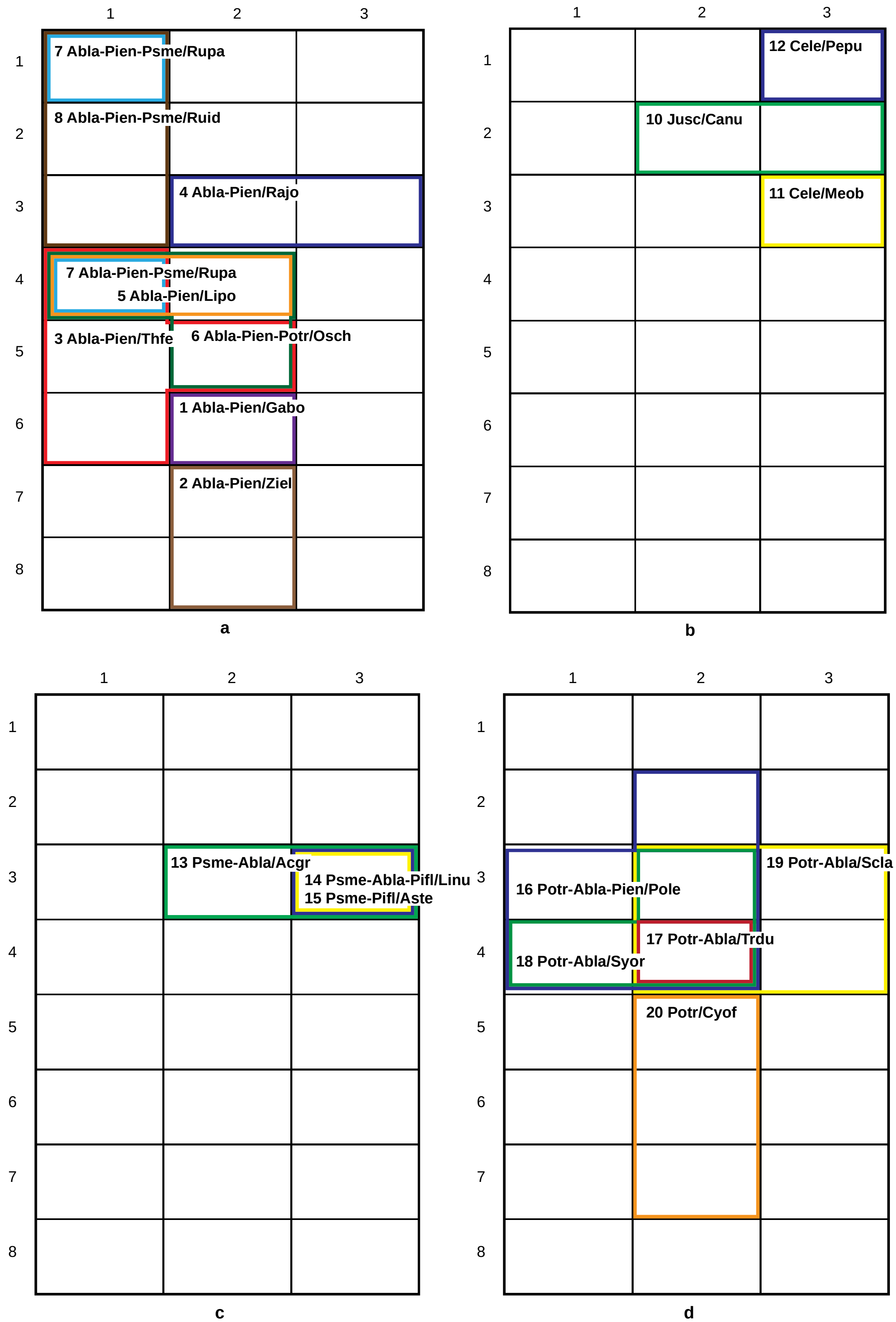


Figure 5.6. Regression of soil pH with K supply rate. Less K is available in a soil solution in high soil pH. The same significant pattern was found for the other essential nutrient supply rates (N, P, Fe).



1
2
3
7 Abla-Pien-Psme/Rupa
8 Abla-Pien-Psme/Ruid
4 Abla-Pien/Rajo
7 Abla-Pien-Psme/Rupa
5 Abla-Pien/Lipo
3 Abla-Pien/Thfe
6 Abla-Pien-Potr/Osch
1 Abla-Pien/Gabo
2 Abla-Pien/Ziel
a
12 Cele/Pepu
10 Jusc/Canu
11 Cele/Meob
b
13 Psme-Abla/Acgr
14 Psme-Abla-Pifl/Linu
15 Psme-Pifl/Aste
c
16 Potr-Abla-Pien/Pole
19 Potr-Abla/Scla
17 Potr-Abla/Trdu
18 Potr-Abla/Syor
20 Potr/Cyof
d

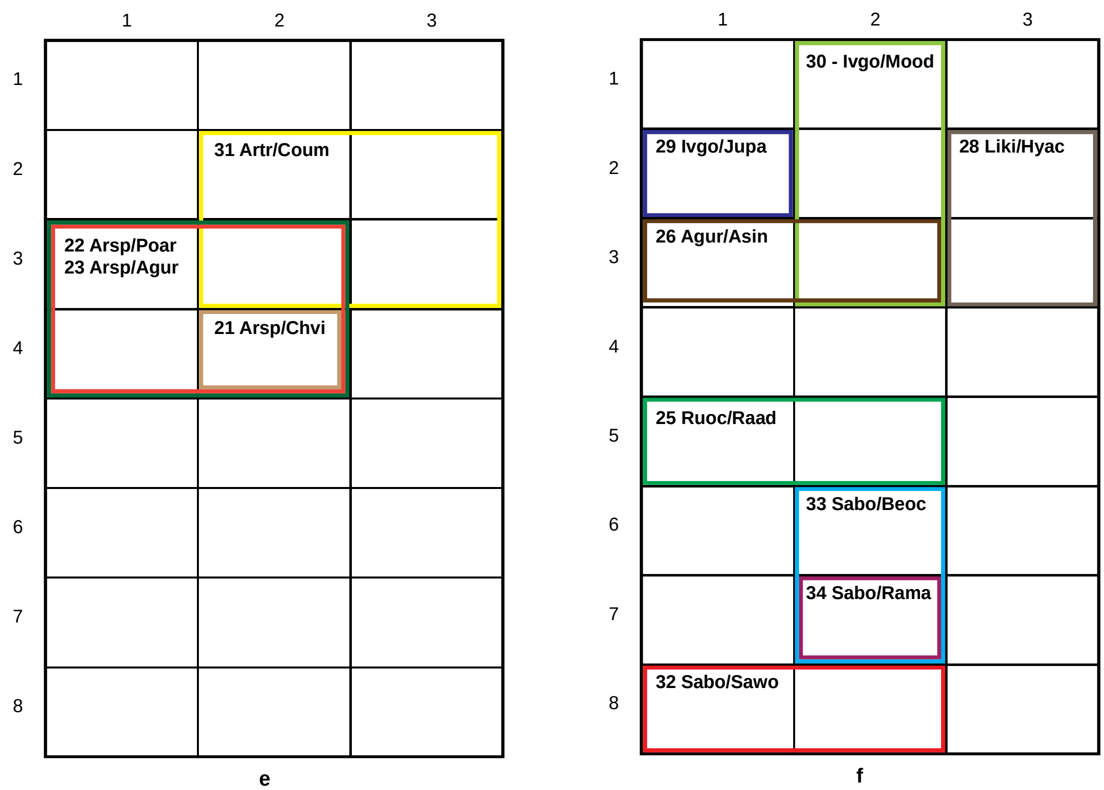


Figure 5.7. Site-vegetation ecological grids showing plant associations and their relation to topography-moisture and fertility. Site classes (1-8 for topography-moisture, 1-3 for fertility) are defined in Table 5.3. Plant associations are defined in Table 5.4.: a) spruce-fir; b) woodland; c) Douglas-fir; d) aspen; e) sagebrush; and f) tall-forb meadows.

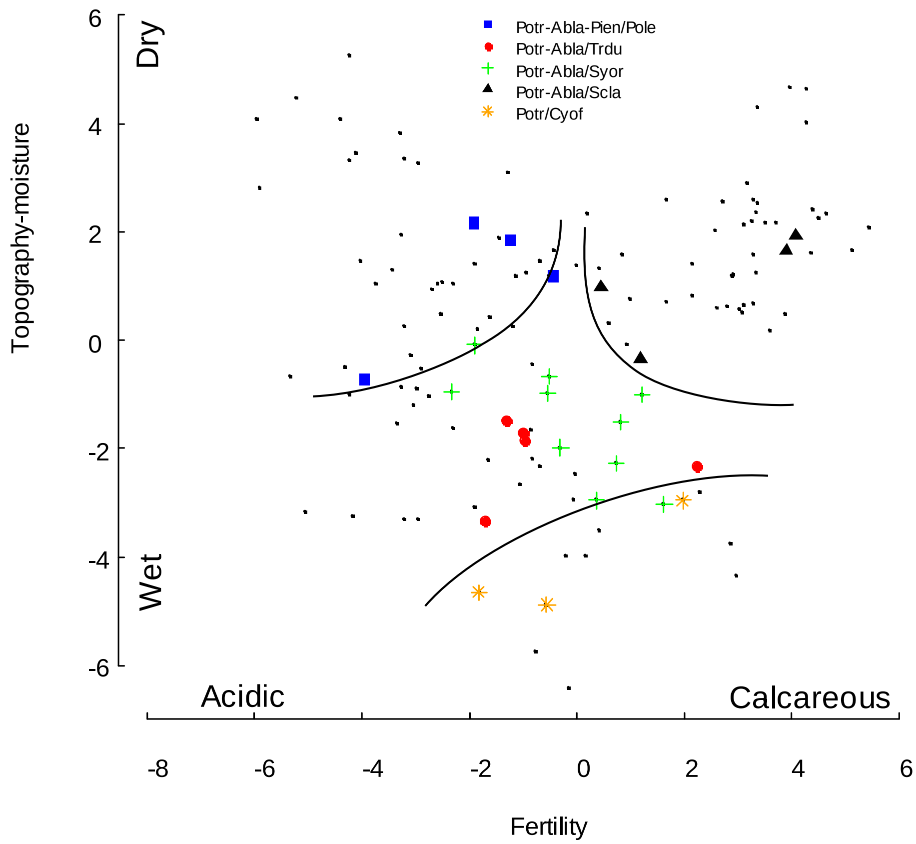


Figure 5.8. Environmental difference among aspen communities projected into a continuous ordination space represented by fertility and topography-moisture axes. Note that the 3x8 dimensional site grid – the site classes (Fig. 5.7) were replaced by continuous ordination scores on both axes. Environmentally discrete communities (poor, wet and alkaline-calcareous) are separated by curves. Environmentally intermediate communities meet in the center. Aspen communities are defined in Table 5.4.

CHAPTER 6

SUMMARY AND CONCLUSIONS

Ecosystem organization

The proposed terrestrial ecosystem classification was developed based on a conceptual framework of ecosystem hierarchical organization. This framework is consistent with the general belief that physical environment (site), represented by climate, soil moisture and soil nutrients, considerably contributes to vegetation distribution. We confirmed the environmental heterogeneity of the study area, derived important environmental gradients influencing ecosystem patterns within that area, and synthesized these gradients into ecologically meaningful levels of ecosystem organization: (1) macroclimate or regional climate; (2) mesoclimate or local climate; and (3) soil fertility.

This organizational structure is consistent with the lower elements of the ECOMAP/TEUI standard and was used as a framework for additional structuring of the organization levels e.g., site classification in building a comprehensive ecosystem classification.

Zonal classification

In order to better understand broad vegetation patterns in a Rocky Mountain landscape, we examined the relationships between vegetation and environmental variables for zonal sites (*sensu* Krajina and Bailey) as represented by sites with mature vegetation, moderate topographic and intermediate soil characteristics. We assessed and classified the response of the complex vegetation to those important environmental factors operating at the highest level of our ecosystem organization - regional climate.

We defined two vegetation geo-climatic zones as areas with the same floristic structure in climatic climax. These zones were: montane with juniper/Douglas-fir; and subalpine with Engelmann spruce/subalpine fir as climatic climax species. We characterized these zones based on climate and landform geomorphology/soils. Regional climate was represented by elevation, precipitation, air and soil temperatures; and geomorphology by zonal soil types. Aspen was excluded from the zonation due its great ecological amplitude. Even stable or climax aspen was not considered as zonal (climatic climax) vegetation.

We argue the vegetation geo-climatic zonation is a conceptual improvement on earlier approaches to vegetation zonation in the region.

Vegetation classification

To answer the question "What are vegetation patterns and important species assemblages in the study area?" we performed a vegetation classification based on the concept of diagnostic species and fidelity. We identified thirty-four vegetation units; for each species, fidelity and constancy was calculated and diagnostic species were identified at the floristic level of plant alliances and associations. These species are useful for recognition of the vegetation units in the field.

Diagnostic species were compared with indicator species of extensive habitat type classification in the central Rocky Mountains. We assumed that diagnostic species are more indicative of the underlying environment than indicator species *sensu* habitat type because they reflect a closer relation of species with the physical environment. Additionally, our vegetation classification describing existing vegetation across a broad range of ecosystems (forest, woodland, riparian, non-forested) reflects vegetation dynamics and may be included as a part of a comprehensive ecosystem classification.

Site classification

In order to better understand the relationship of vegetation with physical environment in the study area, we performed a site classification based on the most important environmental factors and gradients within the subalpine vegetation geo-climatic zone. These gradients were topography-moisture and fertility. We specified important site classes associated with each gradient and constructed a 3x8 dimensional site grid.

We overlaid the existing vegetation classification onto the site classification resulting in allocation of plant associations into the site grid within the subalpine vegetation geo-climatic framework. Based on this allocation, we identify ecosystems as plant associations connected to relatively stable physical environment that is defined by the site grid. Each ecosystem was thus defined by a particular site quality and compared with other ecosystems within the framework of the site grid.

This comprehensive ecosystem classification integrates three independent classifications: zonal (climatic); vegetation; and site classification.

Reflection of the ecosystem classification

The independent classifications synthesized into the comprehensive ecosystem classification provided insight into fundamental ecological questions. We conclude: (1) vegetation zonation is climate based; (2) there are two firm vegetation geo-climatic zones in the study area; (3) thirty-four important plant communities exist in the study area; (4) in addition to climate, there are topography-moisture and soil fertility environmental factors associated with the distribution of vegetation.

There was a remarkable pattern that emerged across the independent classifications; namely that it is very difficult to designate aspen as a consistent ecosystem environmentally. In Chaper 3, aspen could not be distinguished as a separate vegetation geo-climatic zone relative to montane and subalpine zone. In Chapter 4, aspen emerged "fuzzy" floristically as a vegetation unit except in the case of moist and wet communities. In Chapter 5, aspen communities overlap pretty much environmentally, again, except for moist and wet communities, illustrating the broad environmental amplitudes (moisture and fertility) of aspen units. Based on that aspen pattern, we could not find any environmental factor able to clearly separate seral aspen communities from persistent communities in this study. There are probably other factors inherent to aspen that are responsible for its climax or persistent status that are little affected by physical environment.

By integrating three classifications, the comprehensive classification system provides insight into processes and outcomes associated with, for example, disturbance history and changes of ecosystems under climate change. Knowing a plant community's topographical-moisture context and fertility demands, and site vegetation potential, we can assess site disturbance history and vegetation successional status. Additionally, based on knowledge of site properties, we can better estimate potential changes of these properties under different climate change scenarios.

These examples reflect the potential value of a comprehensive classification system. A tool for communication remains its overarching function. The system can be used as an efficient tool not only in ecosystem studies and research but also in applied ecosystem interpretation, planning and management.

APPENDICES

APPENDIX A

ZONAL SOILS PROPERTIES AND CLASSIFICATION

Variables are defined in Table 2.1. Soil description and classification follow Schoeneberger et al. (2002) and Soil Survey Staff (2006).

Plot: FB013; elevation: 2515 m; parent material: glacial till; vegetation: spruce-fir; zone: subalpine

Horizon	Depth (cm)	Color dry	Color moist	Text	pH	Mottles (cm)	RF (%)	Nmin_s (mg/kg soil)	K_s (mg/kg soil)	Ca_s (mg/kg soil)	Mg_s (mg/kg soil)	Mn_d (μg/10 cm^2/6weeks)	C_{ox} (%)	N_{ox} (%)	BS (%)
O	0-5	hemimor													
A	5-9	10YR 5/2	10YR 4/2	scl	5.4		15	9.9	108.0	1018.0	109.0	14.6	1.4	0.0	71
E	9-28	10YR 6/3	10YR 4/4		5.4		10								
Bt1	28-60	10YR 6/4		sc	5.6		50								
Bt2	60-120	10YR 6/4			5.7	60	60								
C	120-130	10YR 5/3					60+								

Eutric Haplocryalfs

Plot: FB014; elevation: 2395 m; parent material: glacial till; vegetation: aspen; zone: subalpine

Horizon	Depth (cm)	Color dry	Color moist	Text	pH	Mottles (cm)	RF (%)	Nmin_s (mg/kg soil)	K_s (mg/kg soil)	Ca_s (mg/kg soil)	Mg_s (mg/kg soil)	Mn_d (μg/10 cm^2/6weeks)	C_{ox} (%)	N_{ox} (%)	BS (%)
A	0-30	7.5YR 3/2	7.5YR 2.5/2	scl	6.1		10	74.3	616.0	2848.0	161.0	2.9	3.7	0.3	66
E	30-55	10YR 6/3	5YR 4/4		6.4		20								
Bt1	55-120	5YR 5/4	5YR 6/4	sc			75								
Bt2	120-130						75								

Typic Argicryolls

Plot: FB015; elevation: 2400 m; parent material: glacial till; vegetation: aspen; zone: subalpine

Horizon	Depth (cm)	Color dry	Color moist	Text	pH	Mottles (cm)	RF (%)	Nmin_s (mg/kg soil)	K_s (mg/kg soil)	Ca_s (mg/kg soil)	Mg_s (mg/kg soil)	Mn_d (μg/10 cm^2/6weeks)	C_{ox} (%)	N_{ox} (%)	BS (%)
A1	0-15	10YR 5/3	10YR 3/3	scl	6.1		+	59.1	1470.0	2597.0	156.0	3.7	3.4	0.3	100
A2	15-30	10YR 5/3	10YR 3/4				+								
EA	30-60	10YR 6/4	10YR 5/4	cl			10								
Bt	60-80			sc		70	15								
BCt	80-100						75+								

Eutric Haplocryalfs

Plot: FB018; elevation: 2155 m; parent material: glacial till; vegetation: spruce-fir; zone: subalpine

Horizon	Depth	Color dry	Color moist	Text	pH	Mottles	RF	Nmin_s	K_s	Ca_s	Mg_s	Mn_d	C_{ox}	N_{ox}	BS
	(cm)					(cm)	(%)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(μg/10 cm^2/6weeks)	(%)	(%)	(%)
O	0-6	resimor													
A	6-15	10YR 4/2-3		scl	6.1		20	25.8	346.0	2708.0	104.0	3.2	2.7	0.2	100
AE	15-25	10YR 4/3	10YR 3/3				30								
E1	25-55	10YR 5/3	10YR 4/3	sl-ls			50								
E2	55-85														
Bt	85-100	10YR 5/3	10YR 5/4	sc			50+								
Mollic	**Palecryalfs**														

Plot: FB022; elevation: 2225 m; parent material: glacial till; vegetation: spruce-fir; zone: subalpine

Horizon	Depth	Color dry	Color moist	Text	pH	Mottles	RF	Nmin_s	K_s	Ca_s	Mg_s	Mn_d	C_{ox}	N_{ox}	BS
	(cm)					(cm)	(%)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(μg/10 cm^2/6weeks)	(%)	(%)	(%)
O	0-11	humimor													
A1	11-14	10YR 4/2	10YR 3/2				10					1.4			
A2	14-16	10YR 4/3	10YR 3-4/2	scl	6.5			31.7	572.0	3116.0	263.0		2.5	0.2	84
AE	16-35	7.5YR 4/3	10YR 4/3				10								
E	35-50	10YR 6/3	10YR 4/3				15								
Bt1	50-80	10YR 5/3	10YR 4/3	sc		50	20								
Bt2	80-100														
Typic	**Haplocryalfs**														

Plot: FB052; elevation: 2780 m; parent material: glacial till; vegetation: spruce-fir; zone: subalpine

Horizon	Depth	Color dry	Color moist	Text	pH	Mottles	RF	Nmin_s	K_s	Ca_s	Mg_s	Mn_d	C_{ox}	N_{ox}	BS
	(cm)					(cm)	(%)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(μg/10 cm^2/6weeks)	(%)	(%)	(%)
O	0-5	lignomor													
A	5-20	10YR 4-5/3			5.7		10	19.6	133.6	1297.8	327.2	5.3	2.0	0.1	83
EA	20-40	10YR 5/4		scl			20								
E	40-60	10YR 6/3					50								
Bt1	60-75	10YR 6/4		sc		75	60								
Bt2	75-95	10YR 6/6					70								
C	95-120						70+								
Typic	**Haplocryalfs**														

Plot: FB057; elevation: 2540 m; parent material: glacial till; vegetation: spruce-fir; zone: subalpine

Horizon	Depth	Color dry	Color moist	Text	pH	Mottles	RF	Nmin_s	K_s	Ca_s	Mg_s	Mn_d	C_{ox}	N_{ox}	BS
	(cm)					(cm)	(%)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(μg/10 cm^2/6weeks)	(%)	(%)	(%)
O	0-8	hemimor													
A	8-35	10YR 5/3	10YR 3/2	scl	5.7			53.6	354.0	2184.0	107.0	3.7	3.3	0.2	100
EB	35-70	10YR 6/3	10YR 5/3				+								
Bt	70-100	10YR 5/3-4	10YR 6/4	sc			+								
C	100-120						50+								
Typic	**Argicryolls**														

Plot: FB059; elevation: 2210 m; parent material: colluvium/till; vegetation: aspen; zone: subalpine

Horizon	Depth	Color dry	Color moist	Text	pH	Mottles	RF	Nmin_s	K_s	Ca_s	Mg_s	Mn_d	C_{ox}	N_{ox}	BS
	(cm)					(cm)	(%)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(µg/10 cm^2/6weeks)	(%)	(%)	(%)
A1	0-15	10YR 4/2	10YR 3/3	cl	6.1		10	73.7	482.0	3329.0	207.0	2.3	5.2	0.4	98
A2	15-45						20								
EB	45-60	10YR 6/3	10YR 5/3				50								
Bt	60-110	10YR 6/4	10YR 6/4	c			50								
BCt	110-120						50+								
Pachic	**Palecryolls**														

Plot: FB063; elevation: 2745 m; parent material: colluvium/quartzite; vegetation: aspen; zone: subalpine

Horizon	Depth	Color dry	Color moist	Text	pH	Mottles	RF	Nmin_s	K_s	Ca_s	Mg_s	Mn_d	C_{ox}	N_{ox}	BS
	(cm)					(cm)	(%)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(µg/10 cm^2/6weeks)	(%)	(%)	(%)
A	0-35	10YR 5/3-4	10YR 4-5/4	scl	5.7		10	30.8	284.0	892.0	88.0		0.5	0.1	85
BE	35-55	7.5YR 5/6	10YR 5/3				20								
Bt	55-75			sc			50								
BCt	75-100						50+								
Eutric	**Haplocryalfs**														

Plot: FB069; elevation: 2390 m; parent material: colluvium; vegetation: aspen; zone: subalpine

Horizon	Depth	Color dry	Color moist	Text	pH	Mottles	RF	Nmin_s	K_s	Ca_s	Mg_s	Mn_d	C_{ox}	N_{ox}	BS
	(cm)					(cm)	(%)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(µg/10 cm^2/6weeks)	(%)	(%)	(%)
A	0-22	10YR 4/3	10YR 3/3	scl	6.3		10	119.5	241.0	3591.0	699.0	0.5	4.7	0.4	100
AE	22-55	10YR 4/4	10YR 3/4												
E	55-70														
Btg	70-100			sc		70									
Typic	**Palecryolls**														

Plot: FB073; elevation: 2510 m; parent material: glacial till/colluvium; vegetation: spruce-fir; zone: subalpine

Horizon	Depth	Color dry	Color moist	Text	pH	Mottles	RF	Nmin_s	K_s	Ca_s	Mg_s	Mn_d	C_{ox}	N_{ox}	BS
	(cm)					(cm)	(%)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(µg/10 cm^2/6weeks)	(%)	(%)	(%)
O	0-10	resimor													
A	10-20	10YR 5/2-3	7.5YR 4/3	sl	6.0			29.9	275.0	1155.0	252.0	8.0	1.3	0.1	100
E	20-32						10								
Bt1	32-50														
Bt2	50-80			scl		50									
BCt	80-100						10+								
Eutric	**Haplocryalfs**														

Plot: FB107; elevation: 2040 m; parent material: colluvium/alluvium; vegetation: aspen; zone: montane

Horizon	Depth	Color dry	Color moist	Text	pH	Mottles	RF	Nmin_s	K_s	Ca_s	Mg_s	Mn_d	C_{ox}	N_{ox}	BS
	(cm)					(cm)	(%)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(µg/10 cm^2/6weeks)	(%)	(%)	(%)
A1	0-20	10YR 4/3	10YR 2/1		6.6			51.7	220.0	2902.0	290.0	1.5	3.3	0.3	83
A2	20-50	10YR 5/3	10YR 2/2	cl											
AE	50-83	10YR 4/3-4	10YR 3/3				+								
Bt1	83-110	7.5YR 4/3	7.5YR 3/3	c											
Bt2	110-130	7.5YR 5/4	7.5YR 4/4												
Pachic	**Palecryolls**														

Plot: FB109; elevation: 2440 m; parent material: colluvium/outwash; vegetation: aspen; zone: subalpine

Horizon	Depth (cm)	Color dry	Color moist	Text	pH	Mottles (cm)	RF (%)	Nmin_s (mg/kg soil)	K_s (mg/kg soil)	Ca_s (mg/kg soil)	Mg_s (mg/kg soil)	Mn_d (µg/10 cm^2/6weeks)	C_{ox} (%)	N_{ox} (%)	BS (%)
A	0-40	10YR 3/2	10YR 2/2	cl	6.7		+	104.2	324.0	6005.0	785.0	1.0	6.6	0.4	96
AB	40-70	10YR 5/3	10YR 4/3				10								
Bt	70-120	10YR 5/4	10YR 4/4	c			40								
BCt	120-130														
Pachic	**Palecryolls**														

Plot: FB110; elevation: 2425 m; parent material: colluvium/outwash; vegetation: aspen; zone: subalpine

Horizon	Depth (cm)	Color dry	Color moist	Text	pH	Mottles (cm)	RF (%)	Nmin_s (mg/kg soil)	K_s (mg/kg soil)	Ca_s (mg/kg soil)	Mg_s (mg/kg soil)	Mn_d (µg/10 cm^2/6weeks)	C_{ox} (%)	N_{ox} (%)	BS (%)
A	0-38	10YR 3/3	10YR 2/2	cl	6.9			58.4	366.0	4487.0	375.0	4.7	4.4	0.3	84
BA	38-62	10YR 5/3	10YR 4/3				+								
Bt1	62-100	10YR 5/4	10YR 4/4	c			+								
Bt2	100-120						10								
Typic	**Palecryolls**														

Plot: FB115; elevation: 2255 m; parent material: colluvium; vegetation: aspen; zone: subalpine

Horizon	Depth (cm)	Color dry	Color moist	Text	pH	Mottles (cm)	RF (%)	Nmin_s (mg/kg soil)	K_s (mg/kg soil)	Ca_s (mg/kg soil)	Mg_s (mg/kg soil)	Mn_d (µg/10 cm^2/6weeks)	C_{ox} (%)	N_{ox} (%)	BS (%)
A	0-30	10YR 3/3	10YR 2/2		6.8			91.8	394.0	3459.0	376.0	2.0	4.3	0.3	80
AE	30-45	10YR 5/2	10YR 3/2	cl			+								
E	45-70	5YR 6/3	5YR 5/2				10								
Bt	70-120	5YR 5/4	5YR 4/4	c			25								
Pachic	**Palecryolls**														

Plot: FB116; elevation: 2480 m; parent material: colluvium; vegetation: aspen; zone: subalpine

Horizon	Depth	Color dry	Color moist	Text	pH	Mottles	RF	Nmin_s	K_s	Ca_s	Mg_s	Mn_d	C_{ox}	N_{ox}	BS
	(cm)					(cm)	(%)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(μg/10 cm^2/6weeks)	(%)	(%)	(%)
A	0-20	10YR 5/3	10YR 3/2-3	scl	6.9		10	89.1		5109.0	452.0	2.9	7.8	0.4	82
EA	20-35	7.5YR 6/3	7.5YR 4/3-4				30								
Bt1	35-50	7.5YR 6/4	7.5YR 5/6	sc	6.5										
Bt2	50-75	5YR 5/6	5YR 4/6				50								
Mollic	**Haplocryalfs**														

Plot: FB127; elevation: 2350 m; parent material: colluvium; vegetation: aspen; zone: subalpine

Horizon	Depth	Color dry	Color moist	Text	pH	Mottles	RF	Nmin_s	K_s	Ca_s	Mg_s	Mn_d	C_{ox}	N_{ox}	BS
	(cm)					(cm)	(%)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(μg/10 cm^2/6weeks)	(%)	(%)	(%)
A1	0-21	10YR 3/2	10YR 2/2		6.0		5	111.4	252.0	5484.0	546.0	2.8	8.8	0.6	88
A2	21-55	10YR 3/2	10YR 3/3	scl			5								
E	55-70	10YR 6/3	10YR 4/4				30								
Bt	70-100	5YR 5/4	5YR 5/6	c			60								
Pachic	**Palecryolls**														

Plot: FB129; elevation: 2245 m; parent material: colluvium; vegetation: aspen; zone: subalpine

Horizon	Depth	Color dry	Color moist	Text	pH	Mottles	RF	Nmin_s	K_s	Ca_s	Mg_s	Mn_d	C_{ox}	N_{ox}	BS
	(cm)					(cm)	(%)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(μg/10 cm^2/6weeks)	(%)	(%)	(%)
A1	0-20	10YR 3/3	10YR 3/3	scl	6.2		10	65.9	220.0	3080.0	209.0	3.4	3.8	0.3	74
A2	20-55	10YR 4/3	10YR 3/3												
EBt	55-70	7.5YR 5/4	7.5YR 4/6	c			30								
Bt	70-100	7.5YR 6/4	7.5YR 5/6				30								
Pachic	**Palecryolls**														

Plot: FB132; elevation: 2465 m; parent material: glacial till; vegetation: aspen; zone: subalpine

Horizon	Depth	Color dry	Color moist	Text	pH	Mottles	RF	Nmin_s	K_s	Ca_s	Mg_s	Mn_d	C_{ox}	N_{ox}	BS
	(cm)					(cm)	(%)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(µg/10 cm^2/6weeks)	(%)	(%)	(%)
A1	0-20	10YR 4/2-3	10YR 3/3	scl	6.3		+	117.7	325.0	2790.0	196.0	1.0	4.3	0.3	74
A2	20-35	10YR 4/3	10YR 3/3				10								
AE	35-60		10YR 3/3				20								
EBt	60-100		10YR 4/4				35								
Bt	100-120		7.5YR 4/6	sicl			35								
Pachic	**Palecryolls**														

Plot: FB134; elevation: 2300 m; parent material: glacial till/colluvium; vegetation: aspen; zone: subalpine

Horizon	Depth	Color dry	Color moist	Text	pH	Mottles	RF	Nmin_s	K_s	Ca_s	Mg_s	Mn_d	C_{ox}	N_{ox}	BS
	(cm)					(cm)	(%)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(µg/10 cm^2/6weeks)	(%)	(%)	(%)
A	0-10	10YR 4/2	10YR 3/3	scl	6.2		10	35.5	295.0	6088.0	575.0	0.4	10.2	0.6	86
AE	10-42	10YR 4/4	10YR 3/3	sc			10								
Bt1	42-75		10YR 3/6	c			15								
Bt2	75-100		10YR 4/4				20								
BCt	100-120		10YR 4/6				20								
Pachic	**Argicryolls**														

Plot: FB136; elevation: 2750 m; parent material: quartzite; vegetation: aspen; zone: subalpine

Horizon	Depth	Color dry	Color moist	Text	pH	Mottles	RF	Nmin_s	K_s	Ca_s	Mg_s	Mn_d	C_{ox}	N_{ox}	BS
	(cm)					(cm)	(%)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(µg/10 cm^2/6weeks)	(%)	(%)	(%)
A	0-20	10YR 5/2	10YR 3/2	scl	5.9		30	45.6		1906.0	128.0	14.2	3.9	0.2	75
Bw	20-50	10YR 6/3	10YR 4/4				60								
Typic	**Haplocryolls**														

Plot: FB140; elevation: 2640 m; parent material: till/quartzite; vegetation: aspen; zone: subalpine

Horizon	Depth (cm)	Color dry	Color moist	Text	pH	Mottles (cm)	RF (%)	Nmin_s (mg/kg soil)	K_s (mg/kg soil)	Ca_s (mg/kg soil)	Mg_s (mg/kg soil)	Mn_d (µg/10 cm^2/6weeks)	C_{ox} (%)	N_{ox} (%)	BS (%)
A1	0-15	10YR 5/3	10YR 3/3	sl	6.0		15	28.7		1178.0	118.0	8.6	1.7	0.1	90
A2	15-37	10YR 5/4	10YR 3/3				30								
Bw	37-56	10YR 6/4	10YR 5/4				50								
BC	56-70	10YR 7/4	10YR 6/4				75+								
Typic	**Haplocryolls**														

Plot: FB141; elevation: 2600 m; parent material: colluvium; vegetation: aspen; zone: subalpine

Horizon	Depth (cm)	Color dry	Color moist	Text	pH	Mottles (cm)	RF (%)	Nmin_s (mg/kg soil)	K_s (mg/kg soil)	Ca_s (mg/kg soil)	Mg_s (mg/kg soil)	Mn_d (µg/10 cm^2/6weeks)	C_{ox} (%)	N_{ox} (%)	BS (%)
A1	0-10	10YR 4/2	10YR 3/2	sc	6.6		10	33.1	120.0	3197.0	158.0	1.2	2.9	0.2	91
A2	10-38	10YR 4/3	10YR 3/3				15								
AE	38-70	10YR 4/4					20								
Bt	70-90	10YR 5/4					20								
C	90-100						30								
Pachic	**Palecryolls**														

Plot: B3; elevation: 2285 m; parent material: colluvium; vegetation: Douglas-fir; zone: montane

Horizon	Depth (cm)	Color dry	Color moist	Text	pH	Mottles (cm)	RF (%)	Nmin_s (mg/kg soil)	K_s (mg/kg soil)	Ca_s (mg/kg soil)	Mg_s (mg/kg soil)	Mn_d (µg/10 cm^2/6weeks)	C_{ox} (%)	N_{ox} (%)	BS (%)
O	0-6	humimor													
A	6-16	10YR 4/3	10YR 3/3	scl	6.6		+	58.6	722.0	4603.0	315.0	0.6	3.5	0.2	100
AE	16-45	10YR 4/4	10YR 3/3				+								
Bt1	45-68	10YR 5/4	10YR 4/4	sc	6.4		10								
Bt2	68-90	10YR 6/3	10YR 5/6				30								
BCt	90-120														
Typic	**Argixerolls**														

Plot: D1; elevation: 2660 m; parent material: Wasatch Formation; vegetation: spruce-fir; zone: subalpine

Horizon	Depth (cm)	Color dry	Color moist	Text	pH	Mottles (cm)	RF (%)	Nmin_s (mg/kg soil)	K_s (mg/kg soil)	Ca_s (mg/kg soil)	Mg_s (mg/kg soil)	Mn_d (µg/10 cm^2/6weeks)	C_{ox} (%)	N_{ox} (%)	BS (%)
O	0-7	humimor													
A	7-12	10YR 4/3	10YR 3/3		6.1		20	22.1	131.0	1542.0	63.0	3.6	1.3	0.0	100
E	15-65	10YR 6/4	7.5YR 4/6	scl			25								
EBt	65-95	7.5YR 6/6	7.5YR 5/8				35								
BCt	95-100						70								
Typic	**Haplocryalfs**														

Plot: D2; elevation: 2685 m; parent material: Wasatch Formation; vegetation: spruce-fir; zone: subalpine

Horizon	Depth (cm)	Color dry	Color moist	Text	pH	Mottles (cm)	RF (%)	Nmin_s (mg/kg soil)	K_s (mg/kg soil)	Ca_s (mg/kg soil)	Mg_s (mg/kg soil)	Mn_d (µg/10 cm^2/6weeks)	C_{ox} (%)	N_{ox} (%)	BS (%)
O	0-7	humimor													
A	7-10	7.5YR 5/3	7.5YR 2.5/3	scl	6.0		20	49.6	235.0	1957.0	84.0	1.8	2.8	0.1	100
E	10-75	7.5YR 5/4	7.5YR 3/4	s			30								
EBt	75-100	7.5YR 6/6	7.5YR 4/6	scl			30								
BCt	100-110	5YR 6/6	5YR 4/6	sc			50								
Typic	**Haplocryalfs**														

Plot: D4; elevation: 2635 m; parent material: Wasatch Formation; vegetation: spruce-fir; zone: subalpine

Horizon	Depth (cm)	Color dry	Color moist	Text	pH	Mottles (cm)	RF (%)	Nmin_s (mg/kg soil)	K_s (mg/kg soil)	Ca_s (mg/kg soil)	Mg_s (mg/kg soil)	Mn_d (µg/10 cm^2/6weeks)	C_{ox} (%)	N_{ox} (%)	BS (%)
O	0-6	lignomor													
A	6-11	10YR 5/4	10YR 3/3		6.6		20	23.9	265.0	1766.0	95.0	4.6	2.9	0.1	100
E	11-55	7.5YR 5/3	7.5YR 3/4	scl			50								
EBt	55-70	7.5YR 6/4	7.5YR 4/4				40								
BCt	70-120	5YR 5/6	5YR 4/6	cl			50								
Typic	**Haplocryalfs**														

Plot: D6; elevation: 2580 m; parent material: Wasatch Formation; vegetation: spruce-fir; zone: subalpine

Horizon	Depth (cm)	Color dry	Color moist	Text	pH	Mottles (cm)	RF (%)	Nmin_s (mg/kg soil)	K_s (mg/kg soil)	Ca_s (mg/kg soil)	Mg_s (mg/kg soil)	Mn_d (µg/10 cm²/6weeks)	C_{ox} (%)	N_{ox} (%)	BS (%)
O	0-5	hemimor													
A	5-8	10YR 4/3	10YR 3/3	scl	6.2		15	20.9	227.0	2136.0	86.0	10.4	1.5	0.1	100
E	8-28	10YR 6/3	10YR 4/4				20								
EBt	28-55	10YR 7/3	10YR 5/4												
Bt	55-105	7.5YR 6/6	7.5YR 4/6	cl			30								
BCt	105-120	5YR6/6	5YR4/6				50+								
Typic	**Haplocryalfs**														

Plot: D8; elevation: 2630 m; parent material: Wasatch Formation; vegetation: spruce-fir; zone: subalpine

Horizon	Depth (cm)	Color dry	Color moist	Text	pH	Mottles (cm)	RF (%)	Nmin_s (mg/kg soil)	K_s (mg/kg soil)	Ca_s (mg/kg soil)	Mg_s (mg/kg soil)	Mn_d (µg/10 cm²/6weeks)	C_{ox} (%)	N_{ox} (%)	BS (%)
O	0-5	humimor													
A	5-9	7.5YR 5/4	7.5YR 3/3	sc	5.7		10	22.7	233.0	2542.0	273.0	0.8	1.5	0.1	100
E	9-28	7.5YR 6/4	10YR 3/4				20								
Bt1	28-60	2.5YR 5/6	2.5YR 4/8	c			10								
Bt2	60-110	2.5YR 5/8	2.5YR 4/8				10								
C	110-120			s			+								
Typic	**Haplocryalfs**														

Plot: R1; elevation: 1920 m; parent material: outwash/colluvium; vegetation: juniper; zone: montane

Horizon	Depth (cm)	Color dry	Color moist	Text	pH	Mottles (cm)	RF (%)	Nmin_s (mg/kg soil)	K_s (mg/kg soil)	Ca_s (mg/kg soil)	Mg_s (mg/kg soil)	Mn_d (µg/10 cm²/6weeks)	C_{ox} (%)	N_{ox} (%)	BS (%)
O	0-1	rhizomull													
A	1-40	10YR 4/2	10YR 2/2	sic	6.6			75.5	732.0	3982.0	637.0	0.8	2.7	0.2	100
AE	40-75	10YR 4-5/3	10YR 3/3												
Bt	75-120	7.5YR 6/6	7.5YR 4/6	c			5								
Pachic	**Argixerolls**														

Plot: SD1; elevation: 1590 m; parent material: outwash/colluvium; vegetation: juniper; zone: montane

Horizon	Depth	Color dry	Color moist	Text	pH	Mottles	RF	Nmin_s	K_s	Ca_s	Mg_s	Mn_d	C_{ox}	N_{ox}	BS
	(cm)					(cm)	(%)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(µg/10 cm^2/6weeks)	(%)	(%)	(%)
A	0-20	10YR 4/2	10YR 3/2	sc	7.0			36.3	517.0	4016.0	628.0	1.2	2.3	0.1	100
AE	20-40	10YR 5/3	10YR 4/3												
Bt	40-60	10YR 5/4	10YR 4/4	c											
Btk	60-90														
Calcic	**Argixerolls**														

Plot: T1; elevation: 1810 m; parent material: outwash/till; vegetation: juniper; zone: montane

Horizon	Depth	Color dry	Color moist	Text	pH	Mottles	RF	Nmin_s	K_s	Ca_s	Mg_s	Mn_d	C_{ox}	N_{ox}	BS
	(cm)					(cm)	(%)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(µg/10 cm^2/6weeks)	(%)	(%)	(%)
O	+	rhizomull													
A	0-35	10YR 4/2	10YR 3/2	sc	6.1		25	38.9	495.0	4688.0	398.0	0.6	3.9	0.3	100
AE	35-50	10YR 5/3	10YR 4/3				40								
Bt	50-60	10YR 6/4	10YR 4/6	c			50+								
Typic	**Argixerolls**														

Plot: T2; elevation: 1820 m; parent material: colluvium; vegetation: Douglas-fir; zone: montane

Horizon	Depth	Color dry	Color moist	Text	pH	Mottles	RF	Nmin_s	K_s	Ca_s	Mg_s	Mn_d	C_{ox}	N_{ox}	BS
	(cm)					(cm)	(%)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(mg/kg soil)	(µg/10 cm^2/6weeks)	(%)	(%)	(%)
O	0-5	hemimor													
A	5-25	10YR 3/2	10YR 2/2	sc	7.2		+	47.2	1335.0	4080.0	401.0	0.4	3.7	0.3	99
AE	25-50	10YR 4/3	10YR 3/3				10								
EBt	50-70	10YR 6/3	10YR 4/6				10								
Bt	70-100	10YR 5/3	10YR 4/4	c			20								
BCt	100-120	10YR 6/6	10YR 5/6				30								
Typic	**Argixerolls**														

Plot: T3; elevation: 1830 m; parent material: colluvium; vegetation: Douglas-fir; zone: montane

Horizon	Depth (cm)	Color dry	Color moist	Text	pH	Mottles (cm)	RF (%)	Nmin_s (mg/kg soil)	K_s (mg/kg soil)	Ca_s (mg/kg soil)	Mg_s (mg/kg soil)	Mn_d (µg/10 cm^2/6weeks)	C_{ox} (%)	N_{ox} (%)	BS (%)
O	0-6	hemimor													
A	6-16	10YR 3/2	10YR 2/2	cl	6.4		10	57.1	415.0	3942.0	306.0	0.4	3.0	0.2	100
AE	16-55	10YR 4/3	10YR 3/3				20								
E	55-100	10YR 5/4	10YR 4/4	c			20								
Bt	100-120	10YR 5/3	10YR 4/3-4				20								
Typic	**Argixerolls**														

Plot: T4; elevation: 1800 m; parent material: outwash/till; vegetation: juniper; zone: montane

Horizon	Depth (cm)	Color dry	Color moist	Text	pH	Mottles (cm)	RF (%)	Nmin_s (mg/kg soil)	K_s (mg/kg soil)	Ca_s (mg/kg soil)	Mg_s (mg/kg soil)	Mn_d (µg/10 cm^2/6weeks)	C_{ox} (%)	N_{ox} (%)	BS (%)
A1	0-20	10YR 4/3	10YR 3/3	sic	6.1		40	35.1	803.0	3141.0	338.0	1.0	2.3	0.2	100
A2	20-38	10YR 5/3	10YR 4/3				50								
AE	38-55	7.5YR 5/4	7.5YR 4/6	c			50								
Bt	55-80						50+								
Typic	**Argixerolls**														

APPENDIX B

PLANT SPECIES LIST

List of 324 vascular plant species recognized in the study area following The Plants database (USDA NRCS 2006) and delimited for Utah (Shultz et al. 2006). >> means accepted name.

Genus/Species	Common name	Authority	Symbol
Abies lasiocarpa	subalpine fir	(Hook.) Nutt.	ABLA
Acer glabrum	Rocky Mountain maple	Torr.	ACGL
Acer grandidentatum	bigtooth maple	Nutt.	ACGR3
Aconitum columbianum	Columbian monkshood	Nutt.	ACCO4
Actaea rubra	red baneberry	(Ait.) Willd.	ACRU2
Agastache urticifolia	nettleleaf giant hyssop	(Benth.) Kuntze	AGUR
Agoseris glauca	pale agoseris	(Pursh) Raf.	AGGL
Agropyron cristatum	crested wheatgrass	(L.) Gaertn.	AGCR
Achillea millefolium	common yarrow	L.	ACMI2
Allium bisceptrum	twincrest onion	S. Wats.	ALBI2
Alnus incana	gray alder	(L.) Moench	ALIN2
Amelanchier alnifolia	Saskatoon serviceberry	(Nutt.) Nutt. ex M. Roemer	AMAL2
Anemone multifida	>>Pulsatilla patens ssp. multifida	(Pritz.) Zamels, non Poir.	ANMU8
Anemone quinquefolia	>>Anemone multifida var. stylosa	L. var. stylosa (A. Nels.) Dutton & Keener	ANQUS
Angelica arguta	Lyall's angelica	Nutt.	ANAR3
Antennaria luzuloides	rush pussytoes	Torr. & Gray	ANLU2
Antennaria microphylla	littleleaf pussytoes	Rydb.	ANMI3
Antennaria parvifolia	small-leaf pussytoes	Nutt.	ANPA4
Apocynum androsaemifolium	spreading dogbane	L.	APAN2
Aquilegia caerulea	Colorado blue columbine	James	AQCA2
Arabis lyallii	Lyall's rockcress	S. Wats.	ARLY
Arabis nuttallii	Nuttall's rockcress	B.L. Robins.	ARNU
Arenaria congesta	ballhead sandwort	Nutt.	ARCO5
Arnica amplexicaulis	clasping arnica	Nutt. var. *piperi* H. St. John & Warren	ARAM2
Arnica cordifolia	heartleaf arnica	Hook.	ARCO9
Arnica chamissonis	Chamisso arnica	Less.	ARCH3
Arnica latifolia	broadleaf arnica	Bong.	ARLA8
Arnica longifolia	spearleaf arnica	D.C. Eat.	ARLO6
Arnica mollis	hairy arnica	Hook.	ARMO4
Artemisia arbuscula	little sagebrush	Nutt.	ARAR8
Artemisia dracunculus	tarragon	L.	ARDR4
Artemisia ludoviciana	white sagebrush	Nutt.	ARLU

Genus/Species	Common name	Authority	Symbol
Artemisia spiciformis	>>Artemisia tridentata ssp. spiciformis	Osterhout	ARSP8
Artemisia tridentata	big sagebrush	Nutt.	ARTR2
Aster ascendens	>>Symphyotrichum ascendens	Lindl.	ASAS5
Aster engelmannii	>>Eucephalus engelmannii	(D.C. Eat.) Gray	ASEN2
Aster foliaceus	>>Symphyotrichum foliaceum var. apricum	Lindl. ex DC. var. apricus Gray	ASFOA
Aster glaucodes	>>Eurybia glauca	Blake	ASGL3
Aster hesperius	>>Symphyotrichum lanceolatum ssp. Hesperium,var.hesperium	Gray	ASHE
Aster integrifolius	>>Eurybia integrifolia	Nutt.	ASIN3
Aster occidentalis	>>Symphyotrichum spathulatum var. spathulatum	(Nutt.) Torr. & Gray	ASOC
Aster pauciflorus	alkali marsh aster	(Nutt.) A. Löve & D. Löve	ALPA14
Aster perelegans	>>Eucephalus elegans	A. Nels. & J.F. Macbr.	ASPE3
Astragalus geyeri	Geyer's milkvetch	A. Gray	ASGE
Astragalus tenellus	looseflower milkvetch	Pursh	ASTE5
Balsamorhiza sagittata	arrowleaf balsamroot	(Pursh) Nutt.	BASA3
Balsamorhiza macrophylla	cutleaf balsamroot	Nutt.	BAMA4
Berberis repens	creeping barberry	Lindl.	BERE
Betula glandulosa	resin birch	Michx.	BEGL
Betula occidentalis	water birch	Hook.	BEOC2
Boykinia jamesii	>>Telesonix heucheriformis	(Torr.) Engl. var. heucheriformis (Rydb.) Engl.	BOJAH
Brickellia californica	California brickellbush	(Torr. & Gray) Gray	BRCA3
Bromus anomalus	nodding brome	Rupr. ex Fourn.	BRAN
Bromus carinatus	>>Bromus marginatus	Hook. & Arn. var. linearis Shear	BRCAL2
Bromus ciliatus	fringed brome	L.	BRCI2
Bromus inermis	smooth brome	Leyss.	BRIN2
Bromus tectorum	cheatgrass	L.	BRTE
Calamagrostis rubescens	pinegrass	Buckley	CARU
Calochortus nuttallii	sego lily	Torr. & Gray	CANU3
Carex atrata	>>Carex heteroneura var. epapillosa	auct. p.p. non L.	CAAT13
Carex geyeri	Geyer's sedge	Boott	CAGE2
Carex haydeniana	cloud sedge	Olney	CAHA6
Carex hoodii	Hood's sedge	Boott	CAHO5
Carex microptera	smallwing sedge	Mackenzie	CAMI7

Genus/Species	Common name	Authority	Symbol
Carex multicostata	manyrib sedge	Mackenzie	CAMU6
Carex nebrascensis	Nebraska sedge	Dewey	CANE2
Carex occidentalis	western sedge	Bailey	CAOC2
Carex pachystachya	chamisso sedge	Cham. ex Steud.	CAPA14
Carex phaeocephala	dunhead sedge	Piper	CAPH2
Carex raynoldsii	Raynolds' sedge	Dewey	CARA6
Carex rossii	Ross' sedge	Boott	CARO5
Carex rostrata	>>Carex utriculata	Stokes var. utriculata (Boott) Bailey	CAROU
Carex xerantica	whitescale sedge	L.H. Bailey	CAXE
Castilleja applegatei	wavyleaf Indian paintbrush	Fern.	CAAP4
Castilleja chromosa	>>Castilleja applegatei ssp. martinii	A. Nels.	CACH7
Castilleja linariifolia	Wyoming Indian paintbrush	Benth.	CALI4
Castilleja miniata	giant red Indian paintbrush	Dougl. ex Hook.	CAMI12
Castilleja occidentalis	western Indian paintbrush	Torr.	CAOC4
Castilleja rhexifolia	splitleaf Indian paintbrush	Rydb.	CARH4
Ceanothus velutinus	snowbrush ceanothus	Dougl. ex Hook.	CEVE
Cercocarpus ledifolius	curl-leaf mountain mahogany	Nutt.	CELE3
Chimaphila umbellata	pipsissewa	(L.) W. Bartram	CHUM
Cirsium calcareum	Cainville thistle	(M.E. Jones) Woot. & Standl.	CICA10
Cirsium eatonii	Eaton's thistle	(Gray) B.L. Robins.	CIEA
Cirsium hookerianum	white thistle	Nutt.	CIHO
Cirsium undulatum	wavyleaf thistle	(Nutt.) Spreng.	CIUN
Claytonia lanceolata	lanceleaf springbeauty	Pall. ex Pursh	CLLA2
Clematis occidentalis	western blue virginsbower	(Hornem.) DC.	CLOC2
Collinsia parviflora	maiden blue eyed Mary	Lindl.	COPA3
Collomia linearis	tiny trumpet	Nutt.	COLI2
Comandra umbellata	bastard toadflax	(L.) Nutt.	COUM
Corallorhiza striata	hooded coralroot	Lindl.	COST
Corallorhiza trifida	yellow coralroot	Chatelain	COTR3
Cornus sericea	redosier dogwood	L.	COSE16
Crepis acuminata	tapertip hawksbeard	Nutt.	CRAC2
Cymopterus hendersonii	>>Pteryxia hendersonii	(Coult. & Rose) Cronq.	CYHE3

Genus/Species	Common name	Authority	Symbol
Cynoglossum officinale	gypsyflower	L.	CYOF
Cystopteris fragilis	brittle bladderfern	(L.) Bernh.	CYFR2
Dactylis glomerata	orchardgrass	L.	DAGL
Delphinium nuttallianum	twolobe larkspur	Pritz. ex Walp.	DENU2
Delphinium occidentale	>>Delphinium occidentale	(S. Wats.) S. Wats. ssp. cucullatum (A. Nels.) Ewan	DEOCC
Descurainia californica	Sierra tansymustard	(Gray) O.E. Schulz	DECA6
Descurainia pinnata	western tansymustard	(Walt.) Britt.	DEPI
Descurainia richardsonii	>>Descurainia incana ssp. incisa	O.E. Schulz ssp. incisa (Engelm.) Detling	DERII
Deschampsia cespitosa	>>Deschampsia caespitosa	(L.) Beauv. [orthographic variant]	DECE
Deschampsia elongata	slender hairgrass	(Hook.) Munro	DEEL
Disporum trachycarpum	roughfruit fairybells	(S. Wats.) Benth. & Hook. f.	DITR2
Draba crassifolia	snowbed draba	Graham	DRCR2
Draba maguirei	Maguire's draba	C.L. Hitchc.	DRMA2
Draba nemorosa	woodland draba	L.	DRNE
Elymus canadensis	Canada wildrye	L.	ELCA4
Elymus cinereus	>>Leymus cinereus	Scribn. & Merr.	ELCI2
Elymus elymoides	squirreltail	(Raf.) Swezey	ELEL5
Elymus glaucus	blue wildrye	Buckl.	ELGL
Elymus lanceolatus	thickspike wheatgrass	(Scribn. & J.G. Sm.) Gould ssp. *lanceolatus*	ELLAL
Elymus scribneri	spreading wheatgrass	(Vasey) M.E. Jones	ELSC4
Elymus spicatus	bluebunch wheatgrass	(Pursh) Gould	ELSP3
Elymus trachycaulus	slender wheatgrass	(Link) Gould ex Shinners	ELTR7
Epilobium angustifolium	>>Chamerion angustifolium ssp. circumvagum	L. ssp. circumvagum Mosquin	EPANC
Epilobium brachycarpum	tall annual willowherb	K. Presl	EPBR3
Epilobium canum	hummingbird trumpet	(Greene) P.H. Raven	EPCA3
Epilobium ciliatum	fringed willowherb	Raf.	EPCI
Equisetum arvense	field horsetail	L.	EQAR
Erigeron eatonii	Eaton's fleabane	Gray	EREA
Erigeron speciosus	aspen fleabane	(Lindl.) DC.	ERSP4
Eriogonum caespitosum	matted buckwheat	Nutt.	ERCA8
Eriogonum heracleoides	parsnipflower buckwheat	Nutt.	ERHE2
Eriogonum umbellatum	sulphur-flower buckwheat	Torr.	ERUM

Genus/Species	Common name	Authority	Symbol
Erysimum asperum	>>Erysimum capitatum var. capitatum	(Nutt.) DC.	ERAS2
Erythronium grandiflorum	yellow avalanche-lily	Pursh	ERGR9
Festuca idahoensis	Idaho fescue	Elmer	FEID
Festuca subulata	bearded fescue	Trin.	FESU
Fragaria vesca	woodland strawberry	L.	FRVE
Fragaria virginiana	Virginia strawberry	Duchesne	FRVI
Frasera speciosa	elkweed	Dougl. ex Griseb.	FRSP
Galium aparine	stickywilly	L.	GAAP2
Galium bifolium	twinleaf bedstraw	S. Wats.	GABI
Galium boreale	northern bedstraw	L.	GABO2
Galium triflorum	fragrant bedstraw	Michx.	GATR3
Geranium richardsonii	Richardson's geranium	Fisch. & Trautv.	GERI
Geranium viscosissimum	sticky purple geranium	Fisch. & C.A. Mey. ex C.A. Mey.	GEVI2
Geum macrophyllum	largeleaf avens	Willd.	GEMA4
Gilia aggregata	>>Ipomopsis aggregata ssp. aggregata	(Pursh) Spreng.	GIAG
Glyceria striata	fowl mannagrass	(Lam.) A.S. Hitchc.	GLST
Goodyera oblongifolia	western rattlesnake plantain	Raf.	GOOB2
Habenaria dilatata	>>Platanthera dilatata var. dilatata	(Pursh) Hook.	HADI7
Habenaria unalascensis	>>Piperia unalascensis	(Spreng.) S. Wats.	HAUN
Hackelia micrantha	Jessica sticktight	(Eastw.) J.L. Gentry	HAMI
Hackelia patens	spotted stickseed	(Nutt.) I.M. Johnston	HAPA
Helianthella uniflora	oneflower helianthella	(Nutt.) Torr. & Gray	HEUN
Heracleum lanatum	>>Heracleum maximum	Michx.	HELA4
Heterotheca villosa	hairy false goldenaster	(Pursh) Shinners	HEVI4
Heuchera parvifolia	littleleaf alumroot	Nutt. ex Torr. & Gray	HEPA11
Heuchera rubescens	pink alumroot	Torr.	HERU
Hieracium albiflorum	white hawkweed	Hook.	HIAL2
Hieracium cynoglossoides	houndstongue hawkweed	Arv.-Touv.	HICY
Holodiscus dumosus	rockspirea	(Nutt. ex Hook.) A. Heller	HODU
Hydrophyllum capitatum	ballhead waterleaf	Dougl. ex Benth.	HYCA4
Hymenoxys acaulis	>>Tetraneuris acaulis var. arizonica	(Pursh) Parker var. arizonica (Greene) Parker	HYACA2
Chaenactis alpina	>>Chaenactis douglasii var. alpina	(Gray) M.E. Jones	CHAL2

Genus/Species	Common name	Authority	Symbol
Chrysothamnus nauseosus	>>Ericameria nauseosa ssp. nauseosa var. speciosa	(Pallas ex Pursh) Britt. ssp. albicaulis (Nutt.) Hall & Clements	CHNAA3
Chrysothamnus viscidiflorus	yellow rabbitbrush	(Hook.) Nutt.	CHVI8
Ivesia gordonii	Gordon's ivesia	(Hook.) Torr. & Gray	IVGO
Juncus balticus	mountain rush	Willd. var. *balticus*	JUBAB2
Juncus ensifolius	swordleaf rush	Wikstr.	JUEN
Juncus mertensianus	Mertens' rush	Bong.	JUME3
Juncus parryi	Parry's rush	Engelm.	JUPA
Juniperus communis	common juniper	L.	JUCO6
Juniperus scopulorum	Rocky Mountain juniper	Sarg.	JUSC2
Koeleria macrantha	prairie Junegrass	(Ledeb.) J.A. Schultes	KOMA
Lathyrus lanszwertii	Nevada pea	Kellogg	LALA3
Lathyrus pauciflorus	fewflower pea	Fern.	LAPA5
Lesquerella multiceps	manyhead bladderpod	Maguire	LEMU2
Leucopoa kingii	spike fescue	(S. Wats.) W.A. Weber	LEKI2
Ligusticum filicinum	fernleaf licorice-root	S. Wats.	LIFI
Ligusticum porteri	Porter's licorice-root	Coult. & Rose	LIPO
Linanthastrum nuttallii	>>Linanthus nuttallii ssp. nuttallii	(Gray) Ewan	LINU4
Linum kingii	King's flax	S. Wats.	LIKI2
Linum lewisii	prairie flax	Pursh	LILE3
Lithophragma parviflorum	smallflower woodland-star	(Hook.) Nutt. ex Torr. & Gray	LIPA5
Lithospermum ruderale	western stoneseed	Dougl. ex Lehm.	LIRU4
Lomatium graveolens	king desertparsley	(S. Wats.) Dorn & Hartman	LOGR6
Lomatium grayi	Gray's biscuitroot	(Coult. & Rose) Coult. & Rose	LOGR
Lonicera involucrata	twinberry honeysuckle	Banks ex Spreng.	LOIN5
Lonicera utahensis	Utah honeysuckle	S. Watson	LOUT2
Lupinus argenteus	silvery lupine	Pursh	LUAR3
Lupinus sericeus	silky lupine	Pursh	LUSE4
Machaeranthera commixta	Bigelow's tansyaster	(A. Gray) Greene var. *commixta* (Greene) B.L. Turner	MABIC
Melica bulbosa	oniongrass	Geyer ex Porter & Coult.	MEBU
Mertensia ciliata	tall fringed bluebells	(James ex Torr.) G. Don	MECI3
Mertensia lanceolata	prairie bluebells	(Pursh) DC. var. *coriacea* (A. Nelson) Higgins & S.L. Welsh	MELAC
Mertensia oblongifolia	oblongleaf bluebells	(Nutt.) G. Don	MEOB

Genus/Species	Common name	Authority	Symbol
Mimulus guttatus	seep monkeyflower	DC.	MIGU
Mitella pentandra	fivestamen miterwort	Hook.	MIPE
Monardella odoratissima	>>Monardella glauca	Benth. ssp. glauca (Greene) Epling	MOODG2
Nemophila breviflora	basin nemophila	Gray	NEBR
Orthocarpus luteus	yellow owl's-clover	Nutt.	ORLU2
Orthocarpus tolmiei	Tolmie's owl's-clover	Hook. & Arn.	ORTO
Osmorhiza chilensis	>>Osmorhiza berteroi, sweetcicely	DC.	OSBE
Osmorhiza occidentalis	western sweetroot	(Nutt. ex Torr. & Gray) Torr.	OSOC
Parnassia fimbriata	fringed grass of Parnassus	Koenig	PAFI3
Paxistima myrsinites	Mountain lover	(Pursh) Raf.	PAMY
Pedicularis groenlandica	elephanthead lousewort	Retz.	PEGR2
Pedicularis racemosa	sickletop lousewort	Dougl. ex Benth.	PERA
Pellaea breweri	Brewer's cliffbrake	D.C. Eat.	PEBR4
Penstemon compactus	compact penstemon	(Keck) Crosswhite	PECO10
Penstemon cyananthus	Wasatch beardtongue	Hook.	PECY2
Penstemon humilis	low beardtongue	Nutt. ex Gray	PEHU
Penstemon leonardii	Leonard's beardtongue	Rydb.	PELE9
Penstemon whippleanus	Whipple's penstemon	Gray	PEWH
Petradoria pumila	grassy rockgoldenrod	(Nutt.) Greene	PEPU7
Petrophytum caespitosum	mat rockspirea	(Nutt.) Rydb.	PECA12
Phacelia hastata	silverleaf phacelia	Dougl. ex Lehm.	PHHA
Phacelia heterophylla	varileaf phacelia	Pursh	PHHE2
Phleum alpinum	alpine timothy	L.	PHAL2
Phleum pratense	timothy	L.	PHPR3
Phlox hoodii	spiny phlox	Richardson	PHHO
Phlox pulvinata	cushion phlox	(Wherry) Cronq.	PHPU5
Picea engelmannii	Engelmann spruce	Parry ex Engelm.	PIEN
Pinus contorta	lodgepole pine	Dougl. ex Loud.	PICO
Pinus flexilis	limber pine	James	PIFL2
Plantago eriopoda	redwool plantain	Torr.	PLER
Plantago lanceolata	narrowleaf plantain	L.	PLLA
Plantago tweedyi	Tweedy's plantain	Gray	PLTW

Genus/Species	Common name	Authority	Symbol
Poa arnowiae	Wasatch bluegrass	Soreng	POAR21
Poa bolanderi	Bolander's bluegrass	Vasey	POBO
Poa bulbosa	bulbous bluegrass	L.	POBU
Poa cusickii	Cusick's bluegrass	Vasey ssp. *epilis* (Scribn.) W.A. Weber	POCUE2
Poa fendleriana	muttongrass	(Steud.) Vasey	POFE
Poa leptocoma	marsh bluegrass	Trin.	POLE2
Poa nervosa/wheeleri	>>Poa wheeleri	(Hook.) Vasey var. wheeleri (Vasey) C.L. Hitchc.	POWH2
Poa pratensis	Kentucky bluegrass	L.	POPR
Poa reflexa	nodding bluegrass	Vasey & Scribn. ex Vasey	PORE
Poa secunda	Sandberg bluegrass	J. Presl	POSE
Polemonium foliosissimum	towering Jacob's-ladder	Gray	POFO
Polygonum bistortoides	American bistort	Pursh	POBI6
Polygonum douglasii	Douglas' knotweed	Greene	PODO4
Polystichum lonchitis	northern hollyfern	(L.) Roth	POLO4
Populus tremuloides	quaking aspen	Michx.	POTR5
Potentilla diversifolia	varileaf cinquefoil	Lehm.	PODI2
Potentilla fruticosa	>>Dasiphora floribunda	auct. non L.	POFR4
Potentilla glandulosa	sticky cinquefoil	Lindl.	POGL9
Potentilla gracilis	slender cinquefoil	Dougl. ex Hook.	POGR9
Prunus virginiana	chokecherry	L.	PRVI
Pseudotsuga menziesii	Douglas-fir	(Mirbel) Franco	PSME
Pterospora andromedea	woodland pinedrops	Nutt.	PTAN2
Purshia tridentata	antelope bitterbrush	(Pursh) DC.	PUTR2
Pyrola asarifolia	liverleaf wintergreen	Michx.	PYAS
Pyrola secunda	>>Orthilia secunda	L.	PYSE
Ranunculus adoneus	alpine buttercup	Gray	RAAD
Ranunculus inamoenus	graceful buttercup	Greene	RAIN
Ranunculus jovis	Utah buttercup	A. Nels.	RAJO
Ranunculus macounii	Macoun's buttercup	Britt.	RAMA2
Ranunculus orthorhynchus	straightbeak buttercup	Hook.	RAOR3
Ribes hudsonianum	northern black currant	Richardson	RIHU
Ribes lacustre	prickly currant	(Pers.) Poir.	RILA

Genus/Species	Common name	Authority	Symbol
Ribes montigenum	gooseberry currant	McClatchie	RIMO2
Ribes oxyacanthoides	Canadian gooseberry	L.	RIOX
Rosa nutkana	Nootka rose	K. Presl	RONU
Rosa woodsii	Woods' rose	Lindl.	ROWO
Rubus idaeus	American red raspberry	L.	RUID
Rubus parviflorus	thimbleberry	Nutt.	RUPA
Rudbeckia occidentalis	western coneflower	Nutt.	RUOC2
Salix bebbiana	Bebb willow	Sarg.	SABE2
Salix boothii	Booth's willow	Dorn	SABO2
Salix drummondiana	Drummond's willow	Barratt ex Hook.	SADR
Salix exigua	narrowleaf willow	Nutt.	SAEX
Salix glauca	grayleaf willow	L.	SAGL
Salix lasiandra	>>Salix lucida ssp. lasiandra	Benth.	SALA5
Salix lutea	yellow willow	Nutt.	SALU2
Salix scouleriana	Scouler's willow	Barratt ex Hook.	SASC
Salix wolfii	Wolf's willow	Bebb	SAWO
Sambucus cerulea	>>Sambucus nigra ssp. cerulea	Raf.	SACE3
Saxifraga odontoloma	brook saxifrage	Piper	SAOD2
Scrophularia lanceolata	lanceleaf figwort	Pursh	SCLA
Sedum debile	orpine stonecrop	S. Wats.	SEDE
Sedum lanceolatum	spearleaf stonecrop	Torr.	SELA
Senecio crassulus	thickleaf ragwort	Gray	SECR
Senecio integerrimus	lambstongue ragwort	Nutt.	SEIN2
Senecio multilobatus	>>Packera multilobata	Torr. & Gray ex Gray	SEMU3
Senecio serra	tall ragwort	Hook.	SESE2
Senecio streptanthifolius	>>Packera streptanthifolia	Greene	SEST3
Senecio triangularis	arrowleaf ragwort	Hook.	SETR
Shepherdia canadensis	russet buffaloberry	(L.) Nutt.	SHCA
Sidalcea oregana	Oregon checkerbloom	(Nutt. ex Torr. & Gray) Gray	SIOR
Silene menziesii	Menzies' campion	Hook.	SIME
Silene oregana	Oregon silene	S. Watson	SIOR3
Smilacina racemosa	>>Maianthemum racemosum ssp. amplexicaule	(L.) Desf. var. amplexicaulis (Nutt.) S. Wats.	SMRAA

Genus/Species	Common name	Authority	Symbol
Smilacina stellata	>>Maianthemum stellatum	(L.) Desf.	SMST
Solidago multiradiata	Rocky Mountain goldenrod	Ait.	SOMU
Solidago nana	baby goldenrod	Nutt.	SONA
Sorbus scopulina	Greene's mountain ash	Greene	SOSC2
Stellaria jamesiana	>>Pseudostellaria jamesiana	Torr.	STJA3
Stellaria nitens	shiny chickweed	Nutt.	STNI
Stipa lettermanii	>>Achnatherum lettermanii	Vasey	STLE4
Stipa nelsonii	>>Achnatherum nelsonii ssp. nelsonii	Scribn.	STNE3
Symphoricarpos oreophilus	mountain snowberry	Gray	SYOR2
Synthyris pinnatifida	featherleaf kittentails	S. Wats.	SYPI
Taraxacum officinale	common dandelion	G.H. Weber ex Wiggers	TAOF
Thalictrum fendleri	Fendler's meadow-rue	Engelm. ex Gray	THFE
Thlaspi montanum	alpine pennycress	L.	THMO5
Tragopogon dubius	yellow salsify	Scop.	TRDU
Trifolium longipes	longstalk clover	Nutt.	TRLO
Trifolium pratense	red clover	L.	TRPR2
Trifolium repens	white clover	L.	TRRE3
Trisetum spicatum	spike trisetum	(L.) K. Richt.	TRSP2
Triteleia grandiflora	largeflower triteleia	Lindl.	TRGR7
Urtica dioica	stinging nettle	L.	URDI
Vaccinium membranaceum	thinleaf huckleberry	Dougl. ex Torr.	VAME
Valeriana edulis	tobacco root	Nutt. ex Torr. & Gray	VAED
Valeriana occidentalis	western valerian	Heller	VAOC2
Veratrum californicum	California false hellebore	Dur.	VECA2
Verbascum thapsus	common mullein	L.	VETH
Veronica biloba	twolobe speedwell	L.	VEBI2
Veronica serpyllifolia	thymeleaf speedwell	L.	VESE
Vicia americana	American vetch	Muhl. ex Willd.	VIAM
Viguiera multiflora	showy goldeneye	(Nutt.) S.F. Blake var. *nevadensis* (A. Nelson) S.F. Blake	VIMUN
Viola adunca	hookedspur violet	Sm.	VIAD
Viola nephrophylla	northern bog violet	Greene	VINE
Viola nuttallii/vallicola	>>Viola vallicola var. vallicola	Pursh ssp. vallicola (A. Nels.) Taylor & MacBryde	VINUV2

Genus/Species	Common name	Authority	Symbol
Viola purpurea	goosefoot violet	Kellogg	VIPU4
Wyethia amplexicaulis	mule-ears	(Nutt.) Nutt.	WYAM
Zigadenus elegans	mountain deathcamas	Pursh	ZIEL2
Zigadenus paniculatus	foothill deathcamas	(Nutt.) S. Wats.	ZIPA2

APPENDIX C

SYNOPTIC TABLE

A part (the first ten vegetation units) of the advanced combined synoptic table with phi coefficient (Fisher's exact test, $p < 0.01$) and constancy (frequency) percentage. The vegetation units are in columns, each row represents one species. The last three rows contain average positive fidelity, No. of faithful species with phi ≥ 40 and species richness for each vegetation unit

Group No.	1	2	3	4	5	6	7	8	9	10
No. of relevés	3	4	6	3	5	5	5	6	5	3
Galium boreale	**62.5** ^{100}	--- ^{25}	--- ·	--- ·	--- ·	--- ^{20}	--- ·	--- ·	--- ·	--- ·
Potentilla gracilis	**49.9** ^{100}	--- ^{25}	--- ^{17}	--- ^{33}	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·
Epilobium ciliatum	**48.5** ^{67}	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·
Potentilla fruticosa	**47.5** ^{67}	--- ^{25}	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·
Stellaria nitens	**44.2** ^{100}	--- ·	18.7 ^{50}	--- ^{33}	--- ^{20}	34.0 ^{80}	--- ^{20}	--- ^{33}	--- ·	--- ·
Salix bebbiana	**42.4** ^{33}	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·
Mertensia ciliata	40.5 ^{100}	--- ·	16.5 ^{50}	--- ^{33}	--- ·	--- ^{20}	--- ·	--- ^{17}	--- ·	--- ·
Zigadenus elegans	--- ·	86.2 ^{100}	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·
Aconitum columbianum	--- ^{33}	69.6 ^{100}	20.3 ^{33}	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·
Senecio triangularis	38.1 ^{67}	59.7 ^{100}	38.1 ^{67}	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·
Arnica amplexicaulis	--- ·	58.8 ^{50}	--- ·	--- ·	--- ^{20}	--- ·	--- ·	--- ·	--- ·	--- ·
Castilleja rhexifolia	--- ·	43.3 ^{75}	--- ^{17}	37.9 ^{67}	--- ·	--- ·	--- ^{40}	27.2 ^{50}	--- ·	--- ·
Ranunculus jovis	--- ·	--- ·	--- ·	**70.8** ^{67}	--- ^{20}	--- ·	--- ·	--- ·	--- ·	--- ·
Senecio crassulus	--- ·	--- ^{25}	--- ^{33}	**42.6** ^{100}	32.6 ^{80}	--- ·	--- ·	--- ^{17}	--- ·	--- ·
Ribes montigenum	--- ·	--- ^{50}	16.9 ^{50}	**41.2** ^{100}	--- ·	--- ^{20}	--- ^{40}	25.0 ^{67}	--- ·	--- ·
Ligusticum porteri	--- ·	--- ·	--- ·	--- ·	**89.2** ^{80}	--- ·	--- ·	--- ·	--- ·	--- ·
Poa bolanderi	--- ·	--- ·	--- ^{17}	--- ^{33}	**81.0** ^{100}	--- ·	--- ·	--- ·	--- ·	--- ·
Rubus parviflorus	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	**77.0** ^{60}	--- ·	--- ·	--- ·
Goodyera oblongifolia	--- ·	--- ^{25}	--- ·	--- ·	--- ·	--- ·	**64.1** ^{60}	--- ·	--- ·	--- ·
Sorbus scopulina	--- ·	--- ·	--- ·	--- ^{33}	24.0 ^{40}	--- ·	**52.5** ^{80}	--- ^{17}	--- ·	--- ·
Chimaphila umbellata	--- ·	--- ·	--- ·	--- ·	--- ^{20}	--- ·	**50.6** ^{40}	--- ·	--- ·	--- ·
Rubus idaeus	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	**70.2** ^{50}	--- ·	--- ·
Carex geyeri	--- ^{33}	--- ·	--- ·	--- ^{33}	--- ·	--- ·	32.0 ^{60}	**56.8** ^{100}	--- ·	--- ·
Poa cusickii	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	**53.5** ^{50}	--- ·	--- ^{33}
Thlaspi montanum	--- ·	--- ·	--- ^{17}	38.8 ^{67}	--- ·	--- ·	--- ·	--- ·	**47.6** ^{80}	--- ·
Calochortus nuttallii	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	**81.0** ^{100}
Juniperus scopulorum	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	**76.7** ^{100}
Lomatium grayi	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	**65.7** ^{67}
Shepherdia canadensis	--- ·	--- ·	--- ·	--- ·	--- ^{20}	--- ·	36.0 ^{60}	--- ·	22.4 ^{40}	--- ·
Lupinus argenteus	--- ·	--- ·	--- ^{33}	27.3 ^{67}	34.1 ^{80}	--- ^{20}	--- ·	--- ^{33}	--- ·	--- ·
Carex pachystachya	37.4 ^{67}	--- ^{25}	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·
Urtica dioica	34.4 ^{67}	--- ·	--- ·	--- ·	--- ·	18.4 ^{40}	--- ·	--- ·	--- ·	--- ·
Erigeron eatonii	--- ·	--- ·	--- ·	32.1 ^{67}	--- ·	--- ·	--- ·	--- ^{33}	28.3 ^{60}	--- ·
Arenaria congesta	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	33.7 ^{67}	--- ^{20}	--- ·
Cystopteris fragilis	--- ·	--- ·	--- ·	--- ^{33}	--- ·	--- ·	--- ^{20}	36.8 ^{50}	--- ·	--- ·
Pyrola secunda	--- ·	--- ^{25}	--- ^{17}	**50.5** ^{100}	27.9 ^{60}	--- ^{40}	**50.5** ^{100}	--- ·	--- ^{20}	--- ·
Angelica arguta	**45.0** ^{67}	**69.6** ^{100}	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·
Salix wolfii	--- ·	**61.7** ^{75}	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·
Pedicularis groenlandica	--- ·	**61.7** ^{75}	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·
Habenaria dilatata	--- ·	**54.3** ^{100}	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·
Aster occidentalis	--- ·	**46.4** ^{100}	--- ^{33}	**46.4** ^{100}	--- ·	--- ·	--- ·	--- ^{17}	--- ·	--- ·
Mimulus guttatus	--- ^{33}	**40.6** ^{75}	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·
Juncus ensifolius	--- ·	39.9 ^{50}	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·
Lonicera utahensis	--- ·	--- ·	--- ^{17}	57.0 ^{100}	32.1 ^{60}	--- ·	**44.5** ^{80}	--- ^{17}	--- ·	--- ·

Group No.	1	2	3	4	5	6	7	8	9	10
No. of relevés	**3**	**4**	**6**	**3**	**5**	**5**	**5**	**6**	**5**	**3**
Arnica latifolia	--- ·	--- ·	--- ^{33}	**51.8**^{100}	--- ·	--- ·	**40.3**^{80}	32.6^{67}	--- ^{40}	--- ·
Hieracium albiflorum	--- ·	--- ·	--- ·	--- ·	**64.1**^{100}	--- ^{20}	**50.4**^{80}	--- ·	--- ·	--- ·
Arnica cordifolia	--- ·	--- ·	27.0^{67}	--- ^{67}	23.7^{60}	--- ·	**44.0**^{100}	27.0^{67}	--- ·	--- ·
Juncus parryi	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	**63.9**^{83}	--- ·	--- ·
Anemone multifida	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	**49.8**^{80}	--- ·
Artemisia arbuscula	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	**47.9**^{100}
Zigadenus paniculatus	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	**45.0**^{67}
Ceanothus velutinus	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	**43.9**^{67}
Equisetum arvense	34.4^{67}	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·
Lonicera involucrata	**42.8**^{100}	**42.8**^{100}	26.1^{67}	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·
Taraxacum officinale	**41.3**^{100}	--- ^{50}	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·
Lathyrus pauciflorus	--- ^{33}	--- ·	--- ·	--- ·	--- ·	--- ^{20}	--- ·	--- ·	--- ·	--- ·
Salix drummondiana	27.8^{67}	32.1^{75}	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·
Veratrum californicum	--- ^{33}	**42.8**^{100}	--- ^{33}	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·	--- ·
Symphoricarpos oreophilus	--- ^{100}	--- ·	--- ^{50}	--- ^{33}	--- ^{60}	--- ^{80}	--- ^{40}	--- ^{83}	--- ^{20}	--- ^{67}
Osmorhiza chilensis	--- ^{100}	--- ^{50}	18.8^{100}	--- ^{100}	18.8^{100}	18.8^{100}	--- ^{80}	--- ^{50}	--- ^{60}	--- ·
Berberis repens	--- ·	--- ·	--- ·	--- ·	--- ·	--- ^{40}	--- ·	--- ·	--- ^{60}	28.3^{100}
Pedicularis racemosa	--- ^{67}	26.7^{100}	26.7^{100}	26.7^{100}	26.7^{100}	--- ^{40}	26.7^{100}	20.4^{83}	26.7^{100}	--- ·
Thalictrum fendleri	--- ^{100}	--- ^{75}	18.0^{100}	--- ^{100}	--- ^{20}	18.0^{100}	--- ^{60}	--- ·	18.0^{100}	--- ·
Paxistima myrsinites	--- ^{33}	--- ^{50}	18.0^{83}	24.1^{100}	--- ^{60}	--- ^{60}	24.1^{100}	24.1^{100}	--- ^{60}	--- ·
Average positive fidelity	**40.4**	**44.4**	**23.9**	**40.7**	**33.0**	**26.2**	**37.7**	**30.4**	**28.9**	**47.3**
No. of faithful spp, phi≥40	**11**	**14**	**0**	**7**	**3**	**0**	**9**	**4**	**2**	**8**
Species richness	**74**	**63**	**71**	**53**	**57**	**72**	**56**	**90**	**49**	**30**

APPENDIX D

ANALYSIS OF THE SYNOPTIC TABLE

The list of diagnostic species for forest vegetation units (1-20) and non-forest vegetation units (21-34). Threshold values: faithful species, phi $\geq$ 40; constant species, frequency $\geq$ 60 %; dominant species, cover $\geq$ 5 %. A digit after a dominant species indicates percentage of relevés in which the species occurs with cover $\geq$ 5 %. Brief habitat characteristics are in Table 4.1, 4.2.

Forest vegetation units

Unit No. 1
Number of relevés: 3

Faithful species: *Galium boreale 62.5, Potentilla gracilis 49.9, Epilobium ciliatum 48.5, Potentilla fruticosa 47.5, Angelica arguta 45.0, Stellaria nitens 44.2, Lonicera involucrata 42.8, Salix bebbiana 42.4, Taraxacum officinale 41.3, Salix boothii 41.1, Mertensia ciliata 40.5*
Constant species: *Abies lasiocarpa 100, Thalictrum fendleri 100, Symphoricarpos oreophilus 100, Rudbeckia occidentalis 100, Picea engelmannii 100, Osmorhiza chilensis 100, Geranium richardsonii 100, Urtica dioica 67, Stellaria jamesiana 67, Smilacina stellata 67, Senecio triangularis 67, Senecio serra 67, Salix drummondiana 67, Rosa woodsii 67, Ribes lacustre 67, Polemonium foliosissimum 67, Pedicularis racemosa 67, Mitella pentandra 67, Geum macrophyllum 67, Equisetum arvense 67, Elymus glaucus 67, Collinsia parviflora 67, Carex pachystachya 67, Aster engelmannii 67, Agastache urticifolia 67, Achillea millefolium 67*
Dominant species: *Picea engelmannii 100, Abies lasiocarpa 67, Salix boothii 33, Ribes lacustre 33, Populus tremuloides 33, Osmorhiza chilensis 33, Equisetum arvense 33, Cornus sericea 33*

Group No. 2
Number of relevés: 4

Faithful species: *Zigadenus elegans 86.2, Angelica arguta 69.6, Aconitum columbianum 69.6, Salix wolfii 61.7, Pedicularis groenlandica 61.7, Senecio triangularis 59.7, Arnica amplexicaulis 58.8, Habenaria dilatata 54.3, Aster occidentalis 46.4, Castilleja rhexifolia 43.3, Veratrum californicum 42.8, Lonicera involucrata 42.8, Salix boothii 41.1, Mimulus guttatus 40.6, Juncus ensifolius 39.9*
Constant species: *Abies lasiocarpa 100, Picea engelmannii 100, Pedicularis racemosa 100, Geranium richardsonii 100, Thalictrum fendleri 75, Salix drummondiana 75, Ligusticum filicinum 75, Frasera speciosa 75, Achillea millefolium 75*
Dominant species: *Picea engelmannii 100, Abies lasiocarpa 75, Veratrum californicum 50, Salix wolfii 50, Geranium richardsonii 50, Arnica amplexicaulis 50, Senecio triangularis 25, Salix boothii 25, Carex microptera 25*

Group No. 3
Number of relevés: 6

Faithful species:
Constant species: *Abies lasiocarpa 100, Thalictrum fendleri 100, Stellaria jamesiana 100, Picea engelmannii 100, Pedicularis racemosa 100, Osmorhiza chilensis 100, Hackelia micrantha 100, Geranium viscosissimum 100, Erythronium grandiflorum 100, Aster engelmannii 100, Aquilegia caerulea 100, Rudbeckia occidentalis 83, Paxistima myrsinites 83, Ligusticum filicinum 83, Hydrophyllum capitatum 83, Carex rossii 83, Achillea millefolium 83, Senecio triangularis 67, Potentilla glandulosa 67, Lonicera involucrata 67, Geranium richardsonii 67, Bromus carinatus 67, Arnica cordifolia 67*
Dominant species: *Abies lasiocarpa 100, Picea engelmannii 100, Rudbeckia occidentalis 50, Arnica cordifolia 33, Thalictrum fendleri 17, Pedicularis racemosa 17, Ligusticum filicinum 17*

Group No. 4
Number of relevés: 3

Faithful species: *Ranunculus jovis 70.8, Lonicera utahensis 57.0, Arnica latifolia 51.8, Pyrola secunda 50.5, Aster occidentalis 46.4, Senecio crassulus 42.6, Ribes montigenum 41.2*
Constant species: *Abies lasiocarpa 100, Thalictrum fendleri 100, Stellaria jamesiana 100, Picea engelmannii 100, Pedicularis racemosa 100, Paxistima myrsinites 100, Osmorhiza chilensis 100, Erythronium grandiflorum 100, Aster engelmannii 100, Aquilegia caerulea 100, Valeriana occidentalis 67, Thlaspi montanum 67, Sedum debile 67, Lupinus argenteus 67, Ligusticum filicinum 67, Geranium viscosissimum 67, Frasera speciosa 67, Erigeron eatonii 67, Claytonia lanceolata 67, Castilleja rhexifolia 67, Carex rossii 67, Arnica cordifolia 67, Achillea millefolium 67*
Dominant species: *Picea engelmannii 100, Arnica latifolia 67, Abies lasiocarpa 33*

Group No. 5
Number of relevés: 5

Faithful species: *Ligusticum porteri 89.2, Poa bolanderi 81.0, Hieracium albiflorum 64.1*
Constant species: *Abies lasiocarpa 100, Viola nuttallii/vallicola 100, Stellaria jamesiana 100, Populus tremuloides 100, Picea engelmannii 100, Pedicularis racemosa 100, Osmorhiza chilensis 100, Ligusticum filicinum 100, Hydrophyllum capitatum 100, Erigeron speciosus 100, Carex rossii 100, Aster engelmannii 100, Achillea millefolium 100, Abies lasiocarpa 100, Senecio serra 80, Senecio crassulus 80, Pseudotsuga menziesii 80, Lupinus argenteus 80, Hackelia micrantha 80, Claytonia lanceolata 80, Aquilegia caerulea 80, Symphoricarpos oreophilus 60, Pyrola secunda 60, Potentilla glandulosa 60, Paxistima myrsinites 60, Osmorhiza occidentalis 60, Lonicera utahensis 60, Bromus carinatus 60, Arnica cordifolia 60*
Dominant species: *Abies lasiocarpa 100, Picea engelmannii 100, Osmorhiza chilensis 100, Ligusticum filicinum 40, Populus tremuloides 20, Pedicularis racemosa 20*

Group No. 6
Number of relevés: 5

Faithful species:
Constant species: *Abies lasiocarpa 100, Thalictrum fendleri 100, Rudbeckia occidentalis 100, Populus tremuloides 100, Osmorhiza chilensis 100, Hydrophyllum capitatum 100, Hackelia micrantha 100, Delphinium nuttallianum 100, Carex rossii 100, Agastache urticifolia 100, Viola nuttallii/vallicola 80, Symphoricarpos oreophilus 80, Stellaria nitens 80, Stellaria jamesiana 80, Smilacina stellata 80, Potentilla glandulosa 80, Polemonium foliosissimum 80, Picea engelmannii 80, Phacelia hastata 80, Geranium viscosissimum 80, Erythronium grandiflorum 80, Elymus glaucus 80, Collomia linearis 80, Bromus carinatus 80, Aster engelmannii 80, Achillea millefolium 80, Senecio serra 60, Ribes lacustre 60, Pseudotsuga menziesii 60, Paxistima myrsinites 60, Galium bifolium 60, Erigeron speciosus 60, Carex hoodii 60*
Dominant species: *Abies lasiocarpa 100, Populus tremuloides 100, Osmorhiza chilensis 80, Picea engelmannii 60, Rudbeckia occidentalis 40, Pseudotsuga menziesii 20, Thalictrum fendleri 20*

Group No. 7
Number of relevés: 5

Faithful species: *Rubus parviflorus 77.0, Goodyera oblongifolia 64.1, Sorbus scopulina 52.5, Chimaphila umbellata 50.6, Pyrola secunda 50.5, Hieracium albiflorum 50.4, Lonicera utahensis 44.5, Arnica cordifolia 44.0, Arnica latifolia 40.3*
Constant species: *Abies lasiocarpa 100, Pseudotsuga menziesii 100, Picea engelmannii 100, Pedicularis racemosa 100, Paxistima myrsinites 100, Aster engelmannii 100, Osmorhiza chilensis 80, Frasera speciosa 80, Aquilegia caerulea 80, Thalictrum fendleri 60, Shepherdia canadensis 60, Sambucus cerulea 60, Pinus flexilis 60, Mitella pentandra 60, Carex rossii 60, Carex geyeri 60*
Dominant species: *Pseudotsuga menziesii 100, Abies lasiocarpa 100, Picea engelmannii 60, Carex geyeri 40, Arnica cordifolia 40, Pyrola secunda 20, Osmorhiza chilensis 20, Arnica latifolia 20*

Group No. 8
Number of relevés: 6

Faithful species: *Rubus idaeus 70.2, Juncus parryi 63.9, Carex geyeri 56.8, Poa cusickii 53.5*
Constant species: *Abies lasiocarpa 100, Picea engelmannii 100, Penstemon leonardii 100, Paxistima myrsinites 100, Aster engelmannii 100, Achillea millefolium 100, Carex geyeri 100, Symphoricarpos oreophilus 83, Pedicularis racemosa 83, Leucopoa kingii 83, Stellaria jamesiana 67, Ribes montigenum 67, Potentilla glandulosa 67, Populus tremuloides 67, Hieracium cynoglossoides 67, Arnica latifolia 67, Arnica cordifolia 67, Arenaria congesta 6, Pseudotsuga menziesii 67*
Dominant species: *Picea engelmannii 100, Carex geyeri 67, Abies lasiocarpa 67, Carex rossii 17*

Group No. 9
Number of relevés: 5

Faithful species: *Anemone multifida 49.8, Thlaspi montanum 47.6*
Constant species: *Abies lasiocarpa 100, Thalictrum fendleri 100, Pinus flexilis 100, Picea engelmannii 100, Penstemon leonardii 100, Pedicularis racemosa 100, Lomatium graveolens 100, Erythronium grandiflorum 100, Aster engelmannii 100, Ribes lacustre 80, Poa fendleriana 80, Leucopoa kingii 80, Claytonia lanceolata 80, Pseudotsuga menziesii 60, Paxistima myrsinites 60, Osmorhiza chilensis 60, Frasera speciosa 60, Erigeron eatonii 60, Castilleja miniata 60, Berberis repens 60*
Dominant species: *Picea engelmannii 100, Pinus flexilis 80, Pseudotsuga menziesii 40, Pedicularis racemosa 20, Aster engelmannii 20*

Group No. 10
Number of relevés: 3

Faithful species: *Calochortus nuttallii 81.0, Juniperus scopulorum 76.7, Lomatium grayi 65.7, Artemisia arbuscula 47.9, Zigadenus paniculatus 45.0, Ceanothus velutinus 43.9, Artemisia tridentata 42.4, Comandra umbellata 41.0*
Constant species: *Juniperus scopulorum 100, Elymus spicatus 100, Berberis repens 100, Balsamorhiza sagittata 100, Symphoricarpos oreophilus 67, Senecio integerrimus 67, Sambucus cerulea 67, Penstemon leonardii 67, Lomatium graveolens 67, Crepis acuminata 67*
Dominant species: *Artemisia arbuscula 100, Juniperus scopulorum 67, Elymus spicatus 67, Balsamorhiza sagittata 33*

Group No. 11
Number of relevés: 3

Faithful species: *Cercocarpus ledifolius 66.7, Mertensia oblongifolia 60.5, Crepis acuminata 59.7, Viola purpurea 59.6, Chrysothamnus viscidiflorus 58.3, Ceanothus velutinus 43.9, Artemisia tridentata 42.4*
Constant species: *Cercocarpus ledifolius 100, Symphoricarpos oreophilus 100, Elymus spicatus 100, Berberis repens 100, Balsamorhiza sagittata 100, Achillea millefolium 100, Thalictrum fendleri 67, Senecio integerrimus 67, Pseudotsuga menziesii 67, Prunus virginiana 67, Pinus flexilis 67, Penstemon leonardii 67, Paxistima myrsinites 67, Helianthella uniflora 67, Aster perelegans 67*
Dominant species: *Symphoricarpos oreophilus 100, Cercocarpus ledifolius 100, Balsamorhiza sagittata 100, Elymus spicatus 67, Chrysothamnus viscidiflorus 33, Aster perelegans 33, Artemisia tridentata 33*

Group No. 12
Number of relevés: 4

Faithful species: *Petradoria pumila 86.3, Cercocarpus ledifolius 66.7, Solidago nana 65.1, Aster ascendens 49.9, Artemisia tridentata 42.4, Comandra umbellata 41.0*
Constant species: *Cercocarpus ledifolius 100, Symphoricarpos oreophilus 100, Leucopoa kingii 100, Eriogonum umbellatum 100, Elymus spicatus 100, Berberis repens 100, Sedum debile 75, Pseudotsuga menziesii 75, Pinus flexilis 75, Penstemon leonardii 75, Machaeranthera commixta 75, Erigeron speciosus 75, Balsamorhiza sagittata 75*
Dominant species: *Cercocarpus ledifolius 100, Elymus spicatus 75, Artemisia arbuscula 50, Solidago nana 25, Prunus virginiana 25, Berberis repens 25, Artemisia tridentata 25*

Group No. 13
Number of relevés: 6

Faithful species: *Acer grandidentatum 53.0, Arnica cordifolia 44.0, Smilacina racemosa 42.1, Viola adunca 40.2*
Constant species: *Abies lasiocarpa 100, Thalictrum fendleri 100, Symphoricarpos oreophilus 100, Stellaria jamesiana 100, Pseudotsuga menziesii 100, Osmorhiza chilensis 100, Hydrophyllum capitatum 100, Hackelia micrantha 100, Elymus glaucus 100, Agastache urticifolia 100, Stellaria nitens 83, Carex rossii 83, Berberis repens 83, Viola nuttallii/vallicola 67, Mitella pentandra 67, Collinsia parviflora 67, Claytonia lanceolata 67, Aster engelmannii 67, Amelanchier alnifolia 67*
Dominant species: *Pseudotsuga menziesii 100, Thalictrum fendleri 83, Osmorhiza chilensis 83, Abies lasiocarpa 50, Berberis repens 33, Symphoricarpos oreophilus 17, Populus tremuloides 17, Elymus glaucus 17, Arnica cordifolia 17*

Group No. 14
Number of relevés: 5

Faithful species: *Linanthastrum nuttallii 51.9, Aster glaucodes 47.9, Acer glabrum 46.5*
Constant species: *Symphoricarpos oreophilus 100, Pseudotsuga menziesii 100, Pinus flexilis 100, Paxistima myrsinites 100, Berberis repens 100, Pedicularis racemosa 80, Leucopoa kingii 80, Aster engelmannii 80, Abies lasiocarpa 60, Picea engelmannii 60, Juniperus communis 60*
Dominant species: *Pseudotsuga menziesii 100, Pinus flexilis 100, Berberis repens 60, Linanthastrum nuttallii 40, Juniperus communis 40, Leucopoa kingii 20, Aster perelegans 20, Aster engelmannii 20, Abies lasiocarpa 20*

Group No. 15
Number of relevés: 3

Faithful species: *Astragalus tenellus 57.2, Bromus anomalus 44.5, Shepherdia canadensis 40.5*
Constant species: *Thalictrum fendleri 100, Symphoricarpos oreophilus 100, Pseudotsuga menziesii 100, Pinus flexilis 100, Phacelia hastata 100, Leucopoa kingii 100, Helianthella uniflora 100, Erigeron speciosus 100, Aster engelmannii 100, Stipa nelsonii 67, Stipa lettermanii 67, Stellaria jamesiana 67, Ribes montigenum 67, Penstemon leonardii 67, Penstemon cyananthus 67, Pedicularis racemosa 67, Osmorhiza chilensis 67, Machaeranthera commixta 67, Lomatium graveolens 67, Hackelia micrantha 67, Geranium viscosissimum 67, Frasera speciosa 67, Castilleja applegatei 67, Berberis repens 67, Balsamorhiza sagittata 67, Aster glaucodes 67, Achillea millefolium 67*
Dominant species: *Pseudotsuga menziesii 100, Pinus flexilis 67, Lomatium graveolens 67, Symphoricarpos oreophilus 33, Leucopoa kingii 33, Eriogonum umbellatum 33, Balsamorhiza sagittata 33, Aster engelmannii 33*

Group No. 16
Number of relevés: 4

Faithful species: *Poa leptocoma 49.4, Lupinus argenteus 44.4, Artemisia ludoviciana 43.8*
Constant species: *Abies lasiocarpa 100, Symphoricarpos oreophilus 100, Stellaria jamesiana 100, Populus tremuloides 100, Picea engelmannii 100, Osmorhiza occidentalis 100, Hydrophyllum capitatum 100, Helianthella uniflora 100, Hackelia micrantha 100, Erigeron speciosus 100, Bromus carinatus 100, Aster engelmannii 100, Senecio serra 75, Phacelia hastata 75, Ligusticum filicinum 75, Galium bifolium 75, Elymus trachycaulus 75, Carex hoodii 75, Artemisia spiciformis 75, Agastache urticifolia 75, Achillea millefolium 75*
Dominant species: *Populus tremuloides 100, Abies lasiocarpa 50, Symphoricarpos oreophilus 25, Pseudotsuga menziesii 25, Picea engelmannii 25, Carex rossii 25, Carex geyeri 25, Bromus carinatus 25, Artemisia ludoviciana 25, Agastache urticifolia 25*

Group No. 17
Number of relevés: 6

Faithful species: *Valeriana occidentalis 45.5, Tragopogon dubius 41.6, Lathyrus pauciflorus 40.0*
Constant species: *Thalictrum fendleri 100, Senecio serra 100, Rudbeckia occidentalis 100, Populus tremuloides 100, Osmorhiza occidentalis 100, Osmorhiza chilensis 100, Elymus glaucus 100, Delphinium occidentale 100, Bromus carinatus 100, Agastache urticifolia 100, Abies lasiocarpa 83, Viola nuttallii/vallicola 83, Symphoricarpos oreophilus 83, Hackelia micrantha 83, Erigeron speciosus 83, Carex hoodii 83, Achillea millefolium 83, Stellaria jamesiana 67, Sidalcea oregana 67, Sambucus cerulea 67, Mertensia ciliata 67, Heracleum lanatum 67, Galium bifolium 67, Collinsia parviflora 67*
Dominant species: *Rudbeckia occidentalis 100, Populus tremuloides 100, Thalictrum fendleri 67, Senecio serra 67, Abies lasiocarpa 67, Lathyrus pauciflorus 50, Bromus carinatus 50, Elymus glaucus 33, Agastache urticifolia 33, Veratrum californicum 17, Osmorhiza occidentalis 17, Osmorhiza chilensis 17, Mertensia ciliata 17, Lathyrus lanszwertii 17, Heracleum lanatum 17*

Group No. 18
Number of relevés: 10

Faithful species:
Constant species: *Thalictrum fendleri 100, Symphoricarpos oreophilus 100, Senecio serra 100, Rudbeckia occidentalis 100, Populus tremuloides 100, Hackelia micrantha 100, Elymus glaucus 100, Carex hoodii 100, Agastache urticifolia 100, Osmorhiza chilensis 90, Delphinium occidentale 90, Bromus carinatus 90, Aster engelmannii 90, Achillea millefolium 90, Osmorhiza occidentalis 80, Lathyrus pauciflorus 80, Abies lasiocarpa 70, Stellaria jamesiana 60, Phacelia hastata 60, Nemophila breviflora 60, Galium bifolium 60, Elymus trachycaulus 60, Delphinium nuttallianum 60, Collomia linearis 60*
Dominant species: *Populus tremuloides 100, Symphoricarpos oreophilus 80, Senecio serra 80, Thalictrum fendleri 60, Agastache urticifolia 60, Rudbeckia occidentalis 50, Lathyrus pauciflorus 40, Elymus glaucus 40, Bromus carinatus 40, Carex hoodii 20, Elymus trachycaulus 10*

Group No. 19
Number of relevés: 4

Faithful species: *Scrophularia lanceolata 55.0, Valeriana occidentalis 45.5, Lathyrus pauciflorus 40.0*
Constant species: *Thalictrum fendleri 100, Symphoricarpos oreophilus 100, Senecio serra 100, Rudbeckia occidentalis 100, Populus tremuloides 100, Phacelia hastata 100, Osmorhiza occidentalis 100, Osmorhiza chilensis 100, Geranium viscosissimum 100, Delphinium occidentale 100, Bromus carinatus 100, Agastache urticifolia 100, Galium bifolium 75, Elymus trachycaulus 75, Elymus glaucus 75, Carex hoodii 75*
Dominant species: *Symphoricarpos oreophilus 100, Populus tremuloides 100, Rudbeckia occidentalis 50, Bromus carinatus 50, Senecio serra 25, Mertensia ciliata 25, Agastache urticifolia 25, Abies lasiocarpa 25*

Group No. 20
Number of relevés: 2

Faithful species: *Cynoglossum officinale 70.9, Dactylis glomerata 63.8, Allium bisceptrum 63.8, Ranunculus orthorhynchus 61.6, Bromus ciliatus 60.3, Carex pachystachya 58.7, Elymus cinereus 55.1, Sidalcea oregana 55.0, Urtica dioica 54.3, Arnica chamissonis 54.3, Geum macrophyllum 51.4, Phleum pratense 48.5, Smilacina stellata 46.7, Trifolium repens 46.4, Veratrum californicum 42.8, Poa reflexa 41.9, Taraxacum officinale 41.3, Lathyrus pauciflorus 40.0*
Constant species: *Thalictrum fendleri 100, Symphoricarpos oreophilus 100, Senecio serra 100, Rudbeckia occidentalis 100, Populus tremuloides 100, Polemonium foliosissimum 100, Osmorhiza occidentalis 100, Osmorhiza chilensis 100, Hackelia micrantha 100, Elymus glaucus 100, Delphinium occidentale 100, Carex hoodii 100, Agastache urticifolia 100, Achillea millefolium 100*, *Veratrum californicum 100, Carex pachystachya 100*, *Elymus cinereus 100*
Dominant species: *Thalictrum fendleri 100, Populus tremuloides 100, Osmorhiza chilensis 100, Veratrum californicum 50, Osmorhiza occidentalis 50, Elymus cinereus 50, Carex pachystachya 50*

Non-forested vegetation unit

Unit No. 21
Number of relevés: 4

Faithful species: *Chrysothamnus viscidiflorus 42.4, Elymus cinereus 40.0*
Constant species: *Symphoricarpos oreophilus 100, Potentilla glandulosa 100, Hackelia micrantha 100, Bromus carinatus 100, Artemisia spiciformis 100, Elymus cinereus 75, Senecio serra 75, Geranium viscosissimum 75, Carex hoodii 75, Agastache urticifolia 75*
Dominant species: *Symphoricarpos oreophilus 100, Artemisia spiciformis 100, Bromus carinatus 50, Elymus cinereus 50, Senecio serra 25, Chrysothamnus viscidiflorus 25, Agastache urticifolia 25*

Group No. 22
Number of relevés: 5

Faithful species: *Poa arnowiae 45.3, Eriogonum heracleoides 44.3, Penstemon cyananthus 44.2*
Constant species: *Symphoricarpos oreophilus 100, Stipa nelsonii 100, Eriogonum umbellatum 100, Artemisia spiciformis 100, Stipa lettermanii 80, Potentilla glandulosa 80, Geranium viscosissimum 80, Bromus carinatus 80, Agastache urticifolia 80, Polemonium foliosissimum 60, Machaeranthera commixta 60, Hieracium cynoglossoides 60, Helianthella uniflora 60, Hackelia micrantha 60, Elymus trachycaulus 60, Delphinium nuttallianum 60, Balsamorhiza sagittata 60, Aster perelegans 60, Achillea millefolium 60*
Dominant species: *Artemisia spiciformis 100, Symphoricarpos oreophilus 80, Eriogonum umbellatum 60, Stipa lettermanii 20, Potentilla glandulosa 20, Bromus carinatus 20, Balsamorhiza sagittata 20*

Group No. 23
Number of relevés: 4

Faithful species:
Constant species: *Symphoricarpos oreophilus 100, Stipa nelsonii 100, Stipa lettermanii 100, Rudbeckia occidentalis 100, Potentilla glandulosa 100, Hackelia micrantha 100, Geranium viscosissimum 100, Eriogonum umbellatum 100, Elymus trachycaulus 100, Bromus carinatus 100, Artemisia spiciformis 100, Agastache urticifolia 100, Stellaria jamesiana 75, Senecio serra 75, Osmorhiza occidentalis 75, Erigeron speciosus 75*
Dominant species: *Agastache urticifolia 100, Rudbeckia occidentalis 75, Potentilla glandulosa 50, Artemisia spiciformis 50, Geranium viscosissimum 50, Symphoricarpos oreophilus 25, Lupinus sericeus 25, Bromus carinatus 75, Eriogonum umbellatum 25, Elymus trachycaulus 25*

Group No. 24
Number of relevés: 3

Faithful species: *Wyethia amplexicaulis 89.1, Poa bulbosa 85.1, Antennaria parvifolia 80.1, Poa secunda 63.6, Artemisia arbuscula 47.9, Koeleria macrantha 46.4, Hieracium cynoglossoides 43.0, Comandra umbellata 41.0*
Constant species: *Symphoricarpos oreophilus 100, Stipa lettermanii 100, Eriogonum umbellatum 100, Artemisia spiciformis 100*
Dominant species: *Wyethia amplexicaulis 67, Artemisia arbuscula 67, Symphoricarpos oreophilus 33, Artemisia spiciformis 33*

Group No. 25
Number of relevés: 4

Faithful species: *Carex multicostata 86.3, Ranunculus adoneus 86.2, Polygonum douglasii 45.6*
Constant species: *Stipa nelsonii 100, Rudbeckia occidentalis 100, Osmorhiza occidentalis 100, Ligusticum filicinum 100, Hackelia micrantha 100, Delphinium occidentale 100, Bromus carinatus 100, Senecio crassulus 75, Osmorhiza chilensis 75, Geranium viscosissimum 75, Galium bifolium 75, Collinsia parviflora 75, Aster integrifolius 75, Agastache urticifolia 75*
Dominant species: *Rudbeckia occidentalis 75, Ranunculus adoneus 75, Ligusticum filicinum 50, Delphinium occidentale 25***,** *Stipa nelsonii 25 , Bromus carinatus 25, Senecio crassulus 25*

Group No. 26
Number of relevés: 4

Faithful species: *Aster integrifolius 52.2, Heuchera parvifolia 51.3, Elymus lanceolatus 47.2*
Constant species: *Osmorhiza occidentalis 100, Hackelia micrantha 100, Geranium viscosissimum 100, Elymus trachycaulus 100, Agastache urticifolia 100, Achillea millefolium 100, Stipa nelsonii 75, Senecio crassulus 75, Potentilla glandulosa 75, Lomatium graveolens 75, Ligusticum filicinum 75, Helianthella uniflora 75, Erythronium grandiflorum 75, Eriogonum umbellatum 75, Erigeron speciosus 75, Bromus carinatus 75, Aster engelmannii 75*
Dominant species: *Agastache urticifolia 50, Rudbeckia occidentalis 25, Potentilla gracilis 25, Osmorhiza occidentalis 25, Lomatium graveolens 25, Helianthella uniflora 25, Geranium viscosissimum 25, Bromus carinatus 25, Artemisia spiciformis 25*

Group No. 27
Number of relevés: 3

Faithful species: *Clematis occidentalis 67.3, Linum kingii 64.1, Linum lewisii 59.3, Penstemon compactus 58.9, Linanthastrum nuttallii 51.9*
Constant species: *Symphoricarpos oreophilus 100, Penstemon leonardii 100, Lomatium graveolens 100, Leucopoa kingii 100, Aster engelmannii 100, Phacelia hastata 67, Helianthella uniflora 67, Berberis repens 67, Aster glaucodes 67*
Dominant species: *Lomatium graveolens 33, Linanthastrum nuttallii 33, Balsamorhiza sagittata 33, Aster glaucodes 33, Berberis repens 33*

Group No. 28
Number of relevés: 6

Faithful species: *Hymenoxys acaulis 91.1, Phlox hoodii 91.0, Synthyris pinnatifida 73.6, Linum kingii 64.1, Phlox pulvinata 63.4, Anemone multifida 63.4, Linum lewisii 59.3, Sedum lanceolatum 57.2, Lesquerella multiceps 57.2, Valeriana edulis 49.3, Penstemon compactus 48.2, Castilleja applegatei 46.6, Monardella odoratissima 45.4, Zigadenus paniculatus 45.0, Erigeron eatonii 41.6, Elymus elymoides 40.3*
Constant species: *Penstemon leonardii 100, Lomatium graveolens 100, Picea engelmannii 83, Solidago multiradiata 67, Ivesia gordonii 67, Elymus trachycaulus 67, Aster engelmannii 67, Arenaria congesta 67, Achillea millefolium 67*
Dominant species: *Linum lewisii 50, Lomatium graveolens 17, Linum kingii 17*

Group No. 29
Number of relevés: 5

Faithful species: *Apocynum androsaemifolium 62.7, Juncus parryi 61.2, Epilobium canum 58.8, Solidago multiradiata 57.9, Arenaria congesta 53.4, Viguiera multiflora 48.4, Ivesia gordonii 45.1, Cystopteris fragilis 44.9, Sedum debile 39.8*
Constant species: *Potentilla glandulosa 100, Penstemon leonardii 100, Eriogonum umbellatum 100, Achillea millefolium 100, Stipa lettermanii 80, Pinus flexilis 80, Erigeron speciosus 80, Carex rossii 80, Leucopoa kingii 60, Elymus trachycaulus 60, Castilleja applegatei 60, Bromus carinatus 60, Berberis repens 60*
Dominant species: *Juncus parryi 20*

Group No. 30
Number of relevés: 5

Faithful species: *Monardella odoratissima 55.6, Eriogonum caespitosum 52.1, Penstemon humilis 48.1, Ivesia gordonii 45.1, Artemisia dracunculus 44.2, Heuchera parvifolia 40.5*
Constant species: *Leucopoa kingii 100, Symphoricarpos oreophilus 80, Stipa lettermanii 80, Penstemon leonardii 80, Machaeranthera commixta 80, Eriogonum umbellatum 80, Potentilla glandulosa 60, Phacelia hastata 60, Helianthella uniflora 60, Geranium viscosissimum 60, Erigeron speciosus 60, Agastache urticifolia 60*
Dominant species: *Monardella odoratissima 80, Eriogonum umbellatum 40, Artemisia dracunculus 20*

Group No. 31
Number of relevés: 6

Faithful species: *Artemisia tridentata 42.4, Comandra umbellata 41.0*
Constant species: *Artemisia tridentata 100, Symphoricarpos oreophilus 100, Elymus spicatus 100, Balsamorhiza sagittata 100, Penstemon leonardii 83, Eriogonum umbellatum 83, Berberis repens 83, Machaeranthera commixta 67, Crepis acuminata 67*
Dominant species: *Artemisia tridentata 100, Elymus spicatus 67, Balsamorhiza sagittata 67, Symphoricarpos oreophilus 17, Poa secunda 17, Chrysothamnus viscidiflorus 17, Ceanothus velutinus 17, Artemisia arbuscula 17, Berberis repens 17*

Group No. 32
Number of relevés: 3

Faithful species: *Carex rostrata 69.6, Carex nebrascensis 69.6, Polygonum bistortoides 57.2, Salix wolfii 54.4, Pedicularis groenlandica 54.4, Juncus ensifolius 54.4, Saxifraga odontoloma 52.8, Juncus balticus 46.1, Salix drummondiana 45.1, Juncus mertensianus 42.4, Deschampsia cespitosa 42.4, Carex raynoldsii 42.4, Betula glandulosa 42.4, Salix boothii 41.1*
Constant species: *Geranium richardsonii 100, Picea engelmannii 67, Mimulus guttatus 67, Lonicera involucrata 67, Habenaria dilatata 67*
Dominant species: *Salix boothii 100, Carex nebrascensis 100, Salix drummondiana 67, Juncus balticus 67, Carex rostrata 33, Betula glandulosa 33*

Group No. 33
Number of relevés: 4

Faithful species: *Betula occidentalis 81.0, Salix lutea 81.0, Juncus balticus 71.2, Carex rostrata 69.6, Carex nebrascensis 69.6, Salix lasiandra 66.7, Salix exigua 66.0, Cornus sericea 58.1, Habenaria dilatata 54.3, Equisetum arvense 54.3*, *Phleum pratense 48.5, Salix drummondiana 45.1, Ranunculus orthorhynchus 44.9, Veratrum californicum 42.8, Salix boothii 41.1, Mimulus guttatus 40.6*
Constant species: *Geranium richardsonii 100*
Dominant species: *Salix lasiandra 100, Salix boothii 100, Carex rostrata 100, Carex nebrascensis 100, Veratrum californicum 75, Salix drummondiana 75, Juncus balticus 75, Salix lutea 25, Equisetum arvense 25, Betula occidentalis 25*

Group No. 34
Number of relevés: 2

Faithful species: *Fragaria virginiana 78.8, Ranunculus macounii 60.3, Trifolium pratense 56.6, Equisetum arvense 54.3, Arnica chamissonis 54.3, Geum macrophyllum 51.4, Smilacina stellata 46.7, Castilleja miniata 46.0, Salix drummondiana 45.1, Veratrum californicum 42.8, Lonicera involucrata 42.8, Poa reflexa 41.9, Taraxacum officinale 41.3, Salix boothii 41.1*
Constant species: *Thalictrum fendleri 100, Rudbeckia occidentalis 100, Osmorhiza chilensis 100, Geranium richardsonii 100, Achillea millefolium 100*
Dominant species: *Salix drummondiana 100, Salix boothii 100, Equisetum arvense 100, Salix lasiandra 50, Ranunculus macounii 50, Geranium richardsonii 50, Betula occidentalis 50*

CURRICULUM VITAE

Antonin Kusbach

Personal information
Department of Wildland Resources and Ecology Center
Utah State University
Email: tony.kusbach@usu.edu

Education

Ph.D.	2006	Ecology	Utah State University
B.S.	1982	Forestry	Mendel University, Brno, Czech Republic

Research interests
Forest ecosystem classification
Application of forest ecosystem classification in ecosystem management

Grants and funding
Kusbach, A., Shaw, J.D. Long, J.N. Forest ecosystem classification in the Intermountain West. Forest Inventory and Analysis Program, USDA Forest Service. 2010-2013.

Awards and honors
North American Forest Ecology Workshop 2009, the best student presentation in section "Ecosystem Classification". http://www.nafew2009.org/

Utah State University, College of Natural Resources, Ecology Center Graduate Research Support Award 2009-2010. http://www.usu.edu/ecology/

Utah State University, College of Natural Resources, Ecology Center Graduate Research Support Award 2007-2008.

Utah State University, Graduate Student Senate, Enhancement Award 2008

Publications (in preparation)
Kusbach, A., H. Van Miegroet, and J.L. Long. Organization of terrestrial ecosystems in the Rocky Mountains, northern Utah.

Kusbach, A., H. Van Miegroet, and J.L. Long. Vegetation geo-climatic zonation in the Rocky Mountains, northern Utah.

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Kusbach, A., J.L. Long, and H. Van Miegroet. Comprehensive ecosystem classification in the Rocky Mountains, northern Utah.

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Frech, I., B. Koch, M. Pospisil, A. **Kusbach**. 2003. Multimedia Geoinformation in Rural Areas with Eco-tourism: The ReGeo-System.

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Kusbach, A., K. Klinka, H. Van Miegroet and J.L. Long. 2008. Ecosystem classification and mapping of the Franklin Basin Watershed, Utah. Poster presented at the 11th North American Forest Soil Conference, June 22-26, Blacksburg, VA. http://www.cpe.vt.edu/nafsc/

Kusbach, A., K. Klinka, H. Van Miegroet and J.L. Long. 2007. "Ecosystem Classification and mapping of the Franklin Basin Watershed" Poster presented at the 6th North American Forest Ecology Workshop. 18-22 June, Vancouver, BC.

Kusbach, A. 2006. Restoring the West 2006: Aspen Restoration, September 12-13, 2006, Logan, UT, field trip and oral presentation.
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